# THE EFFECTS OF WINTER TEMPERATURE AND SHARED NICHE ON POPULATION DYNAMICS OF AUTUMNAL MOTH AND WINTER MOTH

MASTER'S THESIS

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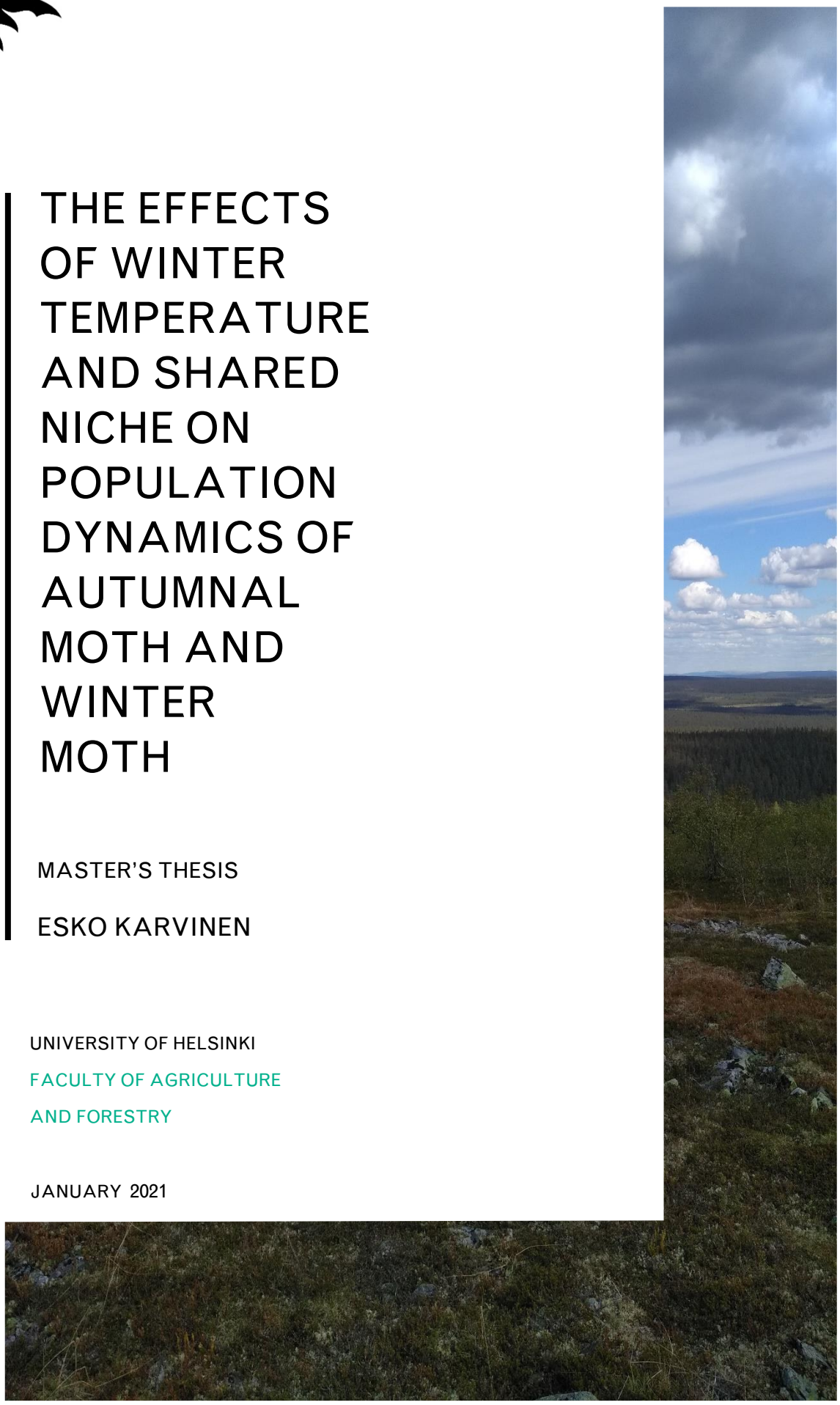

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Tiivistelmä – Referat – Abstract

Climate change will cause an especially pronounced temperature rise in the northern latitudes. These sensitive ecosystems will likely experience significant, rapid, and even irreversible changes. The outbreaks of autumnal moth and winter moth in northern Fennoscandia have already been documented to be prolonged and spread out to new geographical areas. The two species share very similar ecological traits as forest pests, whose population densities fluctuate in approximately ten-year cycles. They can defoliate vast mountain birch forests during the epidemic peaks.

This study focused on jointly analyzing the population dynamics of these two geometrids and the regulatory effects of winter temperatures. The aim was to see whether the populations fluctuate synchronously, does elevation have an effect in species occurrence, and can winter temperature variables be used to model the population development of the species. The study was based on a 33-year long light trap time series from Värriö research station and local climate data from Finnish Meteorological Institute. The data was analyzed with time series analysis methods.

Population fluctuations of autumnal moth and winter moth were observed to be well synchronized regardless of the difference in magnitude of the actual catch numbers. Both species occurred in less numbers with the increase in elevation. Winter moth catch numbers had an increasing trend whereas autumnal moth catch numbers were declining. The trends also differed with elevation. Winter moth was most prominently increasing in mountain birch belt and the decrease in autumnal moth numbers was most significant in traps outside of the mountain birch belt. The regulatory effect of winter temperature variables could be modeled only for winter moth with the methods utilized in this study. The minimum temperatures of December, January, and April seemed to have the most notable effect on the population development. Temperatures in December and January featured the most significant increasing trends based on many different temperature variables examined in this study. This points to the conclusion of winter moth having good potential to increase its abundance in the future.

Avainsanat – Nyckelord – Keywords

autumnal moth, climate change, herbivory, mountain birch, temperature, winter moth

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Tiivistelmä – Referat – Abstract

Ilmastonmuutos nostaa ilmakehän lämpötilaa erityisen paljon pohjoisilla leveysasteilla, joiden häiriöherkät ekosysteemit tulevat todennäköisesti kokemaan merkittäviä, äkkinäisiä ja jopa peruuttamattomia muutoksia. Esimerkiksi pohjoisen Fennoskandian tunturikoivikoissa tavattavien tunturimittarin ja hallamittarin joukkoesiintymien on jo nyt havaittu olevan totuttua pitkäkestoisempia ja levittäytyneen uusille maantieteellisille alueille. Lajit ovat ekologialtaan hyvin samankaltaisia metsätuholaisia, joiden populaatiotiheys on huipussaan noin kymmenen vuoden välein. Epidemiahuippujen aikana ne voivat syödä suuria tunturikoivikkoalueita täysin lehdettömiksi.

Tässä tutkielmassa perehdyttiin tunturimittarin ja hallamittarin keskinäiseen populaatiodynamiikkaan sekä talvilämpötilojen vaikutuksiin dynamiikan taustalla. Tarkoituksena oli selvittää, onko lajien kannanvaihtelu synkronoitunutta, vaikuttaako korkeusvyöhyke lajien esiintymiseen, ja voidaanko talviaikaisilla lämpötilamuuttujilla mallintaa hyönteispopulaatioiden kehitystä. Tutkimus pohjautui Värriön tutkimusasemalla kerättyyn 33-vuotiseen valopyydysaikasarjaan sekä Ilmatieteen laitoksen säätilastoihin paikalliselta havaintopisteeltä. Aineistoa käsiteltiin aikasarja-analyysimenetelmien pohjalta.

Tunturimittarin ja hallamittarin kannanvaihtelun havaittiin olevan synkronoitunutta, vaikka yksilömäärissä olikin merkittävä suuruusluokkaero lajien välillä. Kummankin lajin havaintomäärät vähenivät havaintopaikan korkeuden kasvaessa. Koko aikasarjan matkalla tarkasteltuna hallamittarin havaintomäärissä oli nouseva trendi, kun taas tunturimittarin havaintomäärät olivat laskussa. Trendit olivat kuitenkin hieman toisistaan poikkeavia eri korkeusvyöhykkeillä. Hallamittarihavaintojen lisääntyminen oli erityisen merkittävää nimenomaan tunturikoivikossa ja tunturimittarin väheneminen merkittävintä muualla kuin tunturikoivikossa. Talvilämpötilojen vaikutus kannanvaihteluun pystyttiin tämän tutkielman menetelmillä mallintamaan ainoastaan hallamittarille. Joulu-, tammi-, ja huhtikuun minimilämpötiloilla havaittiin olevan kaikista korostunein säätelevä vaikutus. Joulu- ja tammikuun lämpeneminen olikin tilastojen pohjalta kaikista talvikuukausista huomattavinta useiden tutkittujen lämpötilamuuttujien valossa. Tämä todennäköisesti parantaa hallamittarin runsastumisen mahdollisuuksia tulevaisuudessa.



Avainsanat – Nyckelord – Keywords

hallamittari, herbivoria, ilmastonmuutos, lämpötila, tunturikoivu, tunturimittari

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## FOREWORD

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## TERMS AND ABBREVIATIONS

| | |
|---|---|
| ARIMA | Auto Regressive Integrated Moving Average, a type of a model that incorporates many different temporal structures in time series data (Brownlee 2017). |
| CCF | Cross Correlation Function, a function that compares two time series to see if they are related, a measure of association (Glen 2020a). |
| Chilling period | Requirement for a certain temporal period below a certain temperature threshold (van Asch and Visser 2007). |
| Defoliation | Removal of foliage from a plant (e.g. Pastore et al. 2013). |
| Diapause | State of lowered metabolic activity in order to withstand harsh environmental conditions (van Asch and Visser 2007). |
| Ectothermic | An animal whose body temperature fluctuates according to its surroundings (Kennedy 2019). |

| | |
|---|---|
| Embryogenesis | Development of an embryo within an insect egg, the beginning of the life cycle (Fan et al. 2020). |
| Fennoscandia | Geographic area consisting of Finland, Norway, Sweden and the Kola peninsula in northwestern Russia (Klemola et al. 2010). |
| Herbivore | An animal accustomed to feeding mainly on plant biomass (Crawley 1983). |
| Holarctic | Phytogeographic area encompassing most of the northern hemisphere between North pole and Tropic of Cancer (Tirri et al. 2001). |
| Microclimate | Climate near (up to a few meters from) the ground, strongly affected by the land surface (Rosenberg et al. 1983). |
| Natural enemy | Term used to encompass predatory or pathogenic organisms that consume herbivores (Letourneau et al. 2009). |
| PACF | Partial Autocorrelation Function, a function that depicts how single observations in a time series are correlated with each other at different lags (Nosedal 2019). |
| Phenology | Field of science studying the timing of natural events (van Asch and Visser 2007). |
| Polyphagous | Polyphagous or generalist herbivores can use multiple different food sources, whereas specialists specialize in only certain plants, plant parts or particular plant tissues (Silva and Clarke 2019). |
| Ppm | Parts per million (Tirri et al. 2001). |
| SCP | Supercooling point, the freezing temperature of an organism (Bale 1991). |
| VOC | Volatile Organic Compound, organic atmospheric trace gases other than carbon dioxide and monoxide (Kesselmeier and Staudt 1999). |

# 1. INTRODUCTION

## 1.1 Insects in a changing climate

World's climate has warmed up by a global average of 1 ºC in between 1850 – 2017 as a result of human activities (IPCC 2018). Atmospheric carbon dioxide ($CO_2$) concentration was 100 ppm (parts per million) above pre-industrial levels in 2007 (Denman et al. 2007). Further warming of 0,5 ºC is predicted to be reached between 2030 and 2052 if the rate of temperature increase remains on the current level (IPCC 2018). High latitudes have already experienced the largest rise in temperature in global scale (Parmesan 2006). They are also estimated to experience higher warming rates that are above the global averages both throughout the year and especially in the cold season (Hoegh-Guldberg et al. 2018). Annual mean temperature in the boreal zone (from 60 ºN latitude north) has been predicted to rise with 3,5 – 5 ºC by the end of the 21st century (Lindner et al. 2008; Ammunét et al. 2012).

Insects are expected to react prominently to changes in their physical environment since they are ectothermic organisms (Klapwijk et al. 2013). Environmental conditions affect them directly in dispersal, reproduction, development, and mortality, and indirectly by altering food quality, plant resistance, and interactions with other species (Hodkinson 2005; Netherer and Schopf 2010; Pureswaran et al. 2015). Distribution ranges of insect species are strongly based on temperature and therefore even small changes in temperature can lead to visible changes in their distribution areas (Jepsen et al. 2011). Changes can occur in the form of range expansion or contraction and as altitudinal shifts in species distribution (Hodkinson 2005).

The effects of global warming have already been and will be visible in temporal and spatial dynamics of insect herbivores (Netherer and Schopf 2010). Interactions of plants and insects have been disrupted as interacting species have reacted differently to climate change (Parmesan 2006). This can lead to population extinction if phenological synchrony cannot be returned by natural selection (van Asch and Visser 2007). But the effects can also be positive from the insect's point of view. Bale (1991) classifies natural enemies and competition as the most important factors contributing to insect mortality during summer in the temperate climate zone. He continues to present low temperature

as the main factor during winter. The harsh climate of the boreal zone has traditionally limited the distribution range of many insect pests (Netherer and Schopf 2010). The number of insect outbreaks in boreal forests is now predicted to increase because of the warming climate (Jepsen et al. 2013). Insect outbreaks and large-scale forest defoliation has been seen as one of the most severe effects of climate change in this area (Neuvonen et al. 1999; Karlsen et al. 2013; Vindstad et al. 2019). New disturbance regime will impact the provisioning of goods and services from northern forests (Pureswaran et al. 2015).

Climate change will affect ecosystems and to understand the effects we need to be aware of how climate is linked to ecological processes (Mjaaseth et al. 2005). Studies on the effects of temperature on insect populations will reveal potential changes eventually brought upon by global warming (Peterson and Nilssen 1998). Ecosystems can react to climate change with fast and drastic responses instead of a steady and gradual change (Vindstad et al. 2019). Northern forest ecosystems are especially vulnerable to disturbances because of their simple food webs, slow biological processes, and low species numbers (Sakai et al. 2001; Ammunét et al. 2012). High-latitude tundra and boreal forests thus face a pronounced risk of ecosystem degradation and habitat loss (IPCC 2018).

### 1.2 Autumnal moth and winter moth

Autumnal moth (*Epirrita autumnata* Borkhausen) (Fig 1a) is a forest-defoliating geometrid (Lepidoptera: Geometridae) that is capable of reaching outbreak level population densities in the mountain birch (*Betula pubescens subsp. czerepanovii* [Orlova] Hämet-Ahti) forests covering northwest Europe (Ruohomäki et al. 2000). Its polyphagous larvae feed on over 15 species of deciduous trees, shrubs and dwarf-shrubs focusing mainly on mountain birch (Seppänen 1970 as cited by both Haukioja et al. 1985 and Ruohomäki et al. 2000). Autumnal moth is commonly found in the whole of its holarctic range (Ruohomäki et al. 2000). However, only the mountainous populations of northernmost Europe seem to be capable producing outbreaks in quite regular cycles every nine to ten years (Fig 2) (Tenow 1972 as cited by both Ruohomäki et al. 2000 and Vindstad et al. 2019; Tenow et al. 2007). The number of moth larvae during outbreaks is considerably large. Larval density had been approximately 1000 larvae per $m^2$ of forest floor in Abisko valley outbreak in 1955 (Tenow 1996).

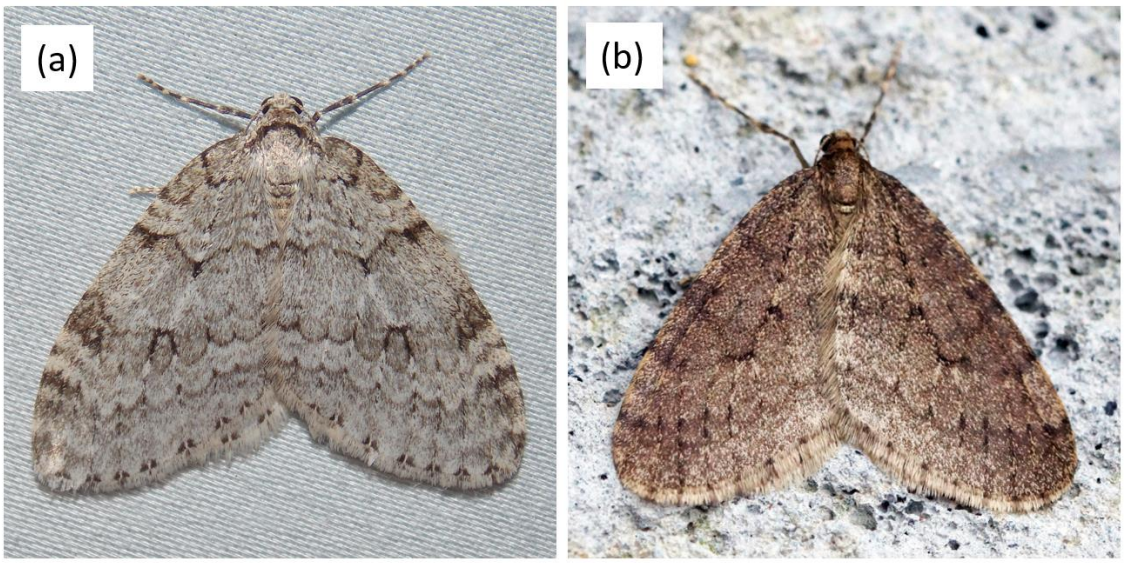


Fig 1. Side-by-side comparison of autumnal moth (a) (Kynd 2013) and winter moth (b) (Sale 2014).

In contrast to autumnal moth, winter moth (*Operophtera brumata* L.) (Fig 1b) can produce outbreaks in a much larger portion of Europe focusing on Central Europe (Tenow et al. 2013). Its main host tree is oak (*Quercus robur* L.) but like autumnal moth, it can adapt to many different host plants such as mountain birch (Tenow et al. 2013). Winter moth cannot tolerate as low winter temperatures as autumnal moth (Tenow 1972 as cited by Bylund 1999) and therefore has not traditionally produced outbreaks in all the same northern regions as autumnal moth. In north, winter moth prefers the more maritime climate west of the Scandes whereas autumnal moth can thrive also in the more eastern continental climate conditions (Tenow et al. 2007). Historical records suggest the expansion of winter moth outbreak area into northeastern Fennoscandia (= east of river Tana) has taken place after 1960s (Tenow 1972 as cited by Hagen et al. 2007).

There is variation in the timing of the life cycle stages throughout geographical occurrence ranges of the two species even though the life cycle per se remains similar (e.g. Holliday 1985; Kimberling and Miller 1988; Peterson and Nilssen 1998). The following description portrays the northernmost populations of Fennoscandia. Both species overwinter as an egg-stage (Bylund 1999). Females lay their eggs in autumn mainly on top of mountain birch trunks and twigs after mating in September or late August (Bylund 1999; Tenow et al. 2007). Eggs are placed separately from one another

(Tenow et al. 2007) beneath lichens, in bark crevices, in forks between shoots, and also more directly exposed to ambient weather conditions (Nilssen and Tenow 1990).

The eggs hatch in spring and the timing is synchronized with mountain birch budburst (Haukioja et al. 1988; Bylund 1999). Feeding habits of winter moth larvae differ from autumnal moth as they spin newly opened leaves together to provide some shelter while feeding (Tenow et al. 2007). Both species go through five larval instars during first part of June and then pupate on forest floor in the end of June or in early July (Tenow 1972 as cited by Bylund 1999; Tenow et al. 2007). The adults eclose in September or late August, after which they are ready to mate (Holliday 1985; Bylund 1999). Pupal stage of winter moth can last until October in some areas (Peterson and Nilssen 1998; Tenow et al. 2007), as they typically eclose about one month later than autumnal moths (Peterson and Nilssen 1998: Vindstad et al. 2019). The late eclosion of winter moth is presumed to be a strategy to avoid generalist predators whereas autumnal moth ecloses earlier in order to avoid being trapped in snow (Hågvar 1976 as cited by Mjaaseth et al. 2005).

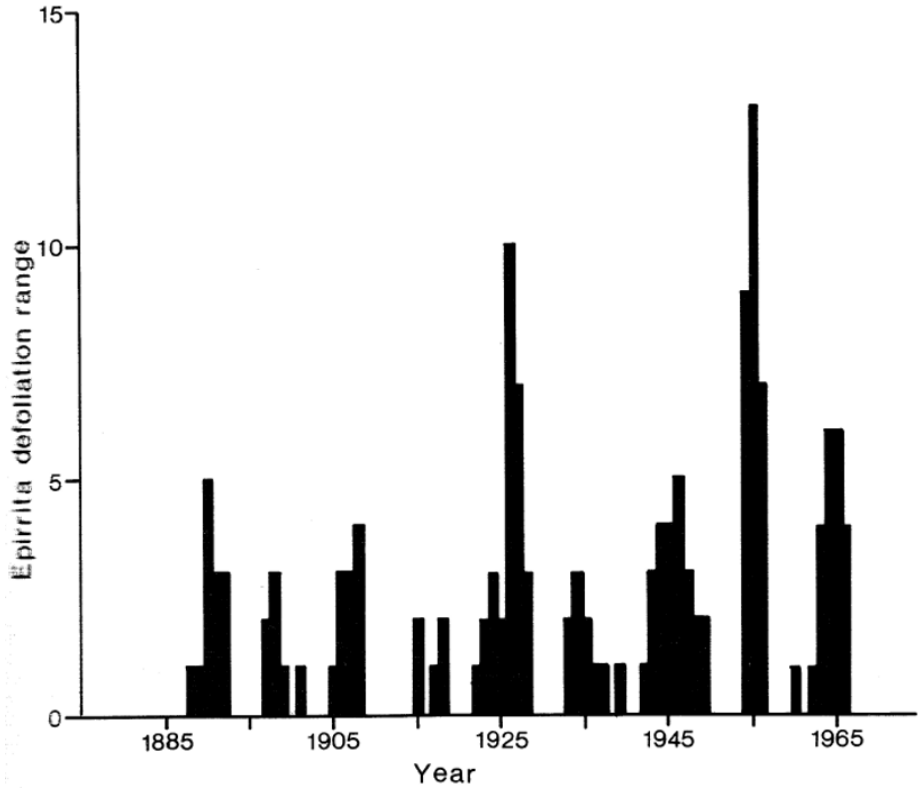


Fig 2. Reported autumnal moth damage (until year 1966) north of the 64º parallel in Fennoscandia illustrating the cyclic population dynamic of the species. Defoliation range depicts defoliation incidence in 0,2º latitudinal belts. (Haukioja et al. 1988 based on Tenow 1972).

### 1.3 Population dynamics of autumnal moth and winter moth

An autumnal moth female can lay an average of 120 eggs (Haukioja et al. 1988) and winter moth is capable of producing an even larger total number of 150 eggs (Holliday 1985). This enables the high potential population growth rates of the species (Haukioja et al. 1988). This theoretical rate of increase is of course reduced by environmental factors affecting fecundity, fertility, and mortality (Haukioja et al. 1988). Virtanen et al. (1998) estimated that it takes at least three consecutive years with high population growth for an autumnal moth outbreak to take place.

Tenow et al. (2007) studied autumnal and winter moth population density development in six locations in northern Fennoscandia during 1990-2003 with focus on temporal synchronization of outbreaks. They noticed how there often (four cases out of six) was a time-lag of one to two years between peak population densities of the two species. Autumnal moth populations would be first to peak followed then by winter moth. Similar observations were reported by Jepsen et al. (2013) who studied outbreaks of autumnal moth and winter moth in northern Norway in 2002-2008. Tenow et al. (2007) also noticed how fluctuations in population density were more synchronous between species when the overall population densities were low. Traditionally autumnal moth outbreaks have lasted for 1-2 consequent years whereas outbreak level population densities of multiple geometrid moth species can last from four to five years (Vindstad et al. 2019). Jepsen et al. (2013) documented a case of autumnal moth and winter moth outbreaks developing in the Varangerfjord area in northern Norway during six consequent years. Outbreaks of geometrid moths have thus been observed to be prolonged and more severe than before (Jepsen et al. 2013; Vindstad et al. 2019).

Population density of a herbivore species often fluctuates in such a way that the peak density tends to collapse before their food plant is completely depleted and unavailable (Haukioja 1980). This can be due to predators, self-regulation of the species itself or functional ecology of the food plant (Haukioja 1980). There are so called density-dependent regulatory factors that start to affect population growth after a certain threshold level of population density is reached (Haukioja et al. 1988). The effect of density-dependent control mechanisms is only seldom direct but more often delayed and visible only after a certain time-lag (Turchin 1990). Explanations for the cyclic population

fluctuations of autumnal moth and winter moth have varied from plant defense mechanisms to parasitism and sunspot activity.

Defense mechanisms of plants can be categorized as constitutive or induced (Haukioja 2005). Constitutive defenses are constantly present whereas induced defense mechanisms activate on herbivore contact (Haukioja 2005). Induced defense mechanisms can be further categorized as rapid induced resistance (RIR) or delayed induced resistance (DIR) (Haukioja et al. 1988). RIR affects the insect generation that triggered the response whereas DIR affects the subsequent generations accentuating population fluctuations (Haukioja 1982 as cited by Haukioja 2005; Haukioja et al. 1988). Haukioja and Niemelä (1977) discovered how mechanical damage to birch leaves affects the development of autumnal moth larvae feeding on undamaged leaves of the same tree individual. The induced effect on nutritional quality of the undamaged leaves could be seen already in a few hours after the mechanical damage occurred (Haukioja and Niemelä 1977; Haukioja 1980). Defoliated birches have intensified chemical defense mechanisms for at least three to four years after a moth outbreak (Haukioja 1980). The relaxation time of the defense mechanisms is long enough to at least partially drive the cyclic population dynamics of geometrid moths (Haukioja 1980; Haukioja et al. 1988) although it cannot explain the dynamics on its own (Haukioja 2005).

Plant defense mechanisms can alter herbivore performance directly via food quality but also indirectly by affecting the likelihood of herbivore predation and parasitism via volatile organic compounds (VOCs) (Haukioja 2005). Lower food quality leads to prolonged larval period which in turn exposes the larvae to a greater probability of parasitism and predatory (Haukioja and Niemelä 1977). Berryman (1996) stated how cyclic population dynamics of forest Lepidoptera are for the most part caused by delayed negative feedback with parasitoids. The dynamics can also be affected by environmental disturbances that influence the Lepidoptera populations (Berryman 1996). More recent research has supported the importance of parasitoids regulating cyclic population dynamics of geometrid moths (e.g. Klemola et al. 2010). It has been speculated whether a higher number of generalist natural enemies prevents autumnal moth outbreaks and cyclic population fluctuations in the southern parts of its occurrence range (Haukioja et al. 1988).

Selås et al. (2004) presented a theory of sunspot activity controlling the cyclic population dynamics of winter moth and autumnal moth. According to them, increased sunspot activity thinners the ozone layer allowing more ultraviolet (UV-B) radiation to enter Earth's surface. Plants would then have to allocate carbon and nutrients to produce chemical compounds needed to protect themselves from the increased radiation. This would decrease the amount of carbon allocated in defensive secondary compounds against herbivores leading to higher survival rate of moth larvae. Sunspot theory has raised debate and faced controversy. Nilssen et al. (2007) highlighted the importance of long-enough time series needed to prove a pattern. Their time series spanned 114 years and did not support the theory described in Selås et al. (2004).

### 1.4 Winter temperature constraints in moth lifecycles

All stages of moth lifecycles are influenced by weather factors and the effects can be not only direct but also indirect via interactions with other species (Bylund 1999). In broader terms, all insects have species-specific levels of cold hardiness i.e. tolerance against cold temperatures (Bale 1987). Especially the increase in winter temperatures has caused autumnal moth to distribute to climatically more continental areas for example in eastern Lapland (Jepsen et al. 2008; Jepsen et al. 2011). For the same reason winter moth has expanded its distribution range from central Europe towards north and east at the same time as its already existing northern distribution sites have increased in size (Jepsen et al. 2008; Ammunét et al. 2012). Climatically continental areas such as Forest Lapland have not traditionally experienced as regular outbreak cycles as some other parts of autumnal moth outbreak range (Virtanen et al. 1998). This is because of low minimum temperatures being lethal for the overwintering eggs (Nilssen and Tenow 1990).

The traditional concept of survival in cold temperatures classifies insects as either freeze tolerant or freeze avoiding (Bale 1996). Freeze tolerance and avoidance are based on such biochemical compounds as ice nucleating agents, polyols and antifreeze proteins (Bale 1996). Ice nucleating agents restrict freezing to take place in somewhat safe extra cellular spaces, polyols lower the supercooling point and antifreeze proteins protect from freezing especially in autumn and spring (Bale 1996). Overwintering autumnal and winter moth eggs experience this kind of physiological and biochemical changes in autumn in order to increase their supercooling ability (Nilssen and Tenow 1990). Bale (1991) defined

supercooling as the process of lowering the freezing temperature i.e. supercooling point (SCP) of an organism.

SCP of moth eggs varies from early to late winter because of diapause and embryogenesis (Nilssen and Tenow 1990). Diapause is a way of resisting harsh environmental conditions by decreasing ongoing metabolic activity (van Asch and Visser 2007). It prevents the eggs from starting the hatching development in autumn even if environmental conditions could be similar to spring (van Asch and Visser 2007). Diapause is also an important tool in maintaining synchrony between herbivore and its host plant (Hodkinson 2005). Climate change can desynchronize herbivore and its host plant if they react to climate change in a different way (Parmesan 2007; van Asch and Visser 2007). Warmer temperature has caused winter moth eggs to hatch before oak (*Quercus robur* L.) budburst in some areas, which has forced winter moth to shift to other host species (Visser and Holleman 2001). Diapause can be a tool in avoiding this kind of asynchronous development.

Autumnal moth eggs begin diapause in autumn and finish it in mid-January to switch to embryogenesis (Nilssen and Tenow 1990). Consequently, SCP of autumnal moth eggs ranges from -34,9 to -36,5 ºC in early winter during diapause and rises to a range from -28,3 to -29,8 ºC in February with the start of embryogenesis (Nilssen and Tenow 1990). Ammunét et al. (2012) reported an averaged critical temperature for autumnal moth on diapausal stage to be -36,8 ºC with the lowest tolerated temperature being -37,7 ºC based on their laboratory experiment.

There has been ongoing debate whether winter moth eggs have diapause or not with the possible conclusion that some populations have it and other (mainly southern) ones do not (e.g. Holliday 1985; van Asch and Visser 2007). For examples of the controversy, Salis et al. (2016) stated that winter moth eggs in the Netherlands do not have diapause while Visser and Holleman (2001) claimed the eggs, also in Netherlands, switch from diapause to embryogenesis in late February. Kimberling and Miller (1988) studied the effect of a possible diapause on the timing of winter moth egg hatch. They tested how the thermal requirements for hatching change during winter and found no significant change after mid-January. They explained this with a diapause that would end in mid-January (Kimberling and Miller 1988). Ammunét et al. (2012) also suggested towards the existence of diapause with no commentary on its temporal scope.

MacPhee (1967 as cited by Nilssen and Tenow 1990) determined an average SCP for winter moth to be -35 ºC in Nova Scotia, Canada. Laboratory experiment by Ammunét et al. (2012) resulted in an averaged critical temperature of -36,1 ºC during diapause with the lowest tolerated temperature being -37,1 ºC. They used eggs of Fennoscandian origin in their study. The SCP determined by MacPhee (1967) most likely refers to the diapausal egg-stage as well. There currently is no research on winter moth temperature tolerance in the post-diapausal stage of embryogenesis, probably because of the controversy surrounding the sole existence of the diapause.

Minimum temperature per se is not the only factor causing mortality for autumnal moth eggs during winter (Virtanen et al. 1998) and actual freezing is not the only lethal effect of cold temperature (Bale 1987). It is important to take into account both the extreme temperatures exceeding SCP and the duration of temperatures not necessarily exceeding the SCP of an insect (Bale 1991, -1996). Temperature below the SCP kills organisms almost instantly whereas prolonged temperatures below zero but not below the SCP can still lead to cumulative cryoinjuries and eventual death (Bale 1991).

MacPhee (1967 as cited by Tenow 1996) stated that most winter moth eggs will freeze even after 16-hour exposure to -33 ºC even though their SCP is -35 ºC. Ammunét et al. (2012) conducted a field study where they monitored survival rates of moth eggs on three different sites while simultaneously recording minimum temperatures. They reported how the survival probability of winter moth eggs was already down to approximately 30 % in sites where minimum temperatures reached -33 ºC and down to around 0 % in minimum temperatures exceeding -35 ºC on two sites out of three. Survival probability for autumnal moth was still around 70-80 % in -34 ºC minimum temperature on two sites out of three (Ammunét et al. 2012). Nilssen and Tenow (1990) noted that autumnal moth can tolerate longer cold spells than winter moth, which seems to be in accordance with the findings of Ammunét et al. (2012) discussed above.

### 1.5 Altitudinal differences in outbreaks

Many environmental factors change with the change in altitude. Such factors include temperature, precipitation, wind speed, atmospheric turbulence, radiation input and partial pressure of atmospheric gases (Hodkinson 2005). It is estimated for temperature

to decrease 5,5-6,5 ºC in an ascent of 1000 meters (Anslow and Shawn 2002 as cited by Hodkinson 2005). Overall structural complexity of habitats decreases with increasing altitude (Hodkinson 2005).

Winter moth prefers lower and middle altitudes and autumnal moth higher slopes when they produce outbreaks in the same area (Hågvar 1976 as cited by Bylund 1999; Tenow 1996). This is most likely due to microclimatic conditions that affect the timing of birch budburst (Bylund 1999) as hatching of winter moth eggs seems to be better adapted and synchronized to earlier mountain birch budburst (Tenow 1972 as cited by Tenow 1996). Larvae hatching too early before budburst can starve in the lack of food whereas larvae hatching too late will suffer from low food quality as the nutritional quality of birch leaves deteriorates quickly as they grow (Haukioja 1980; Haukioja et al. 1988). It is also possible that winter moth tries to avoid the more probable early snowfall of higher altitudes by preferring lower parts of slopes, as it can be detrimental for its late eclosing adults (Mjaaseth et al. 2005). Autumnal moth can concurrently favor higher altitudes to avoid generalist predators, which are probably more abundant in lower altitudes during its adult period earlier in the autumn (Mjaaseth et al. 2005). However, winter moth outbreaks in the 21st century have started to occur in the same (higher) altitudinal zones as autumnal moth outbreaks before that (Hagen et al. 2007). This is most likely linked to climate warming. It can ease the pressure of generalist predators on winter moth populations.

Mountain birch individuals in the lowest parts of fell slopes in valleys with water courses have often been observed to avoid defoliation even in landscapes otherwise damaged by outbreak (Nilssen and Tenow 1990). This is reportedly to do with cold air accumulating in valleys instead of the higher parts of fell slopes (Tenow 1975 as cited by Nilssen and Tenow 1990). Cloud-free sky conditions cause strong radiation inversion that allows the accumulation of cold air into valleys via slope winds flowing down the fell sides (Virtanen et al. 1998). This mechanism can distinguish between defoliated areas and areas with no defoliation, but it is unlikely the driver of the reported altitudinal segregation of the two species (Hagen et al. 2007).

### 1.6 Effects of herbivory in mountain birch forests

Mountain birch (Fig 3) is a low stature tree or a polycormic (i.e. many-stemmed) shrub that forms the tree line (Fig 4) in northern Fennoscandia (Bylund 1999; Haukioja 2003). Mountain birch is a hybrid species resulting from introgression of dwarf birch (*Betula nana* L.) and white birch (*Betula pubenscens* Ehrh.) (Kallio et al 1983 as cited by Haukioja 2003). Especially the polycormic mountain birch individuals are capable of efficient production of basal shoots to reduce damage suffered from stem and root dieback (Bylund 1999). They also utilize dormant buds to produce new shoots (Haukioja 2003). Old forest stands are particularly prone to moth outbreaks (Bylund 1997; Ruohomäki et al. 1997 as cited by Tenow et al. 2007).

Defoliators do not usually kill their host plants instantly but cumulative damage over several years can lead to increased tree mortality (Tenow 1972 as cited by Jepsen et al. 2013; Haukioja and Niemelä 1977). Vindstad et al. (2019) found there to be a threshold level in defoliation intensity (a mean drop in Normalized Difference Vegetation Index of more than 4 % during outbreak) after which tree mortality was notably increased. They also reported that forest recovery was weaker in areas that had experienced more severe defoliation during a moth outbreak. They explained this with positive feedbacks provided by living trees. Living trees can act as seed trees, provide protection from harsh weather conditions, attract herbivores to feed on them instead of the new seedlings, reduce the amount of sunlight on seedlings to reduce the need for transpired water, and maintain the mycorrhizae network that promotes seedling growth. However, they did not see any of these factors to be explanatory enough on its own.

Lehtonen and Heikkinen (1995) reported that mountain birch forest recovery via new shoots can be weaker than expected because of the decay of the dead tree trunks. New shoots often utilize the root system of their original trunk before growing their own. Rot can thus spread to the new tree individuals causing untimely mortality (Lehtonen and Heikkinen 1995). Reindeer browsing in mountain birch forests (Skogland 1984) can feed on mountain birch leaves and prefer to browse on basal sprouts (Haukioja and Heino 1974 as cited by Tenow 1996). This can delay forest regeneration after moth outbreaks (Kallio and Lehtonen 1973; Tenow 1996).

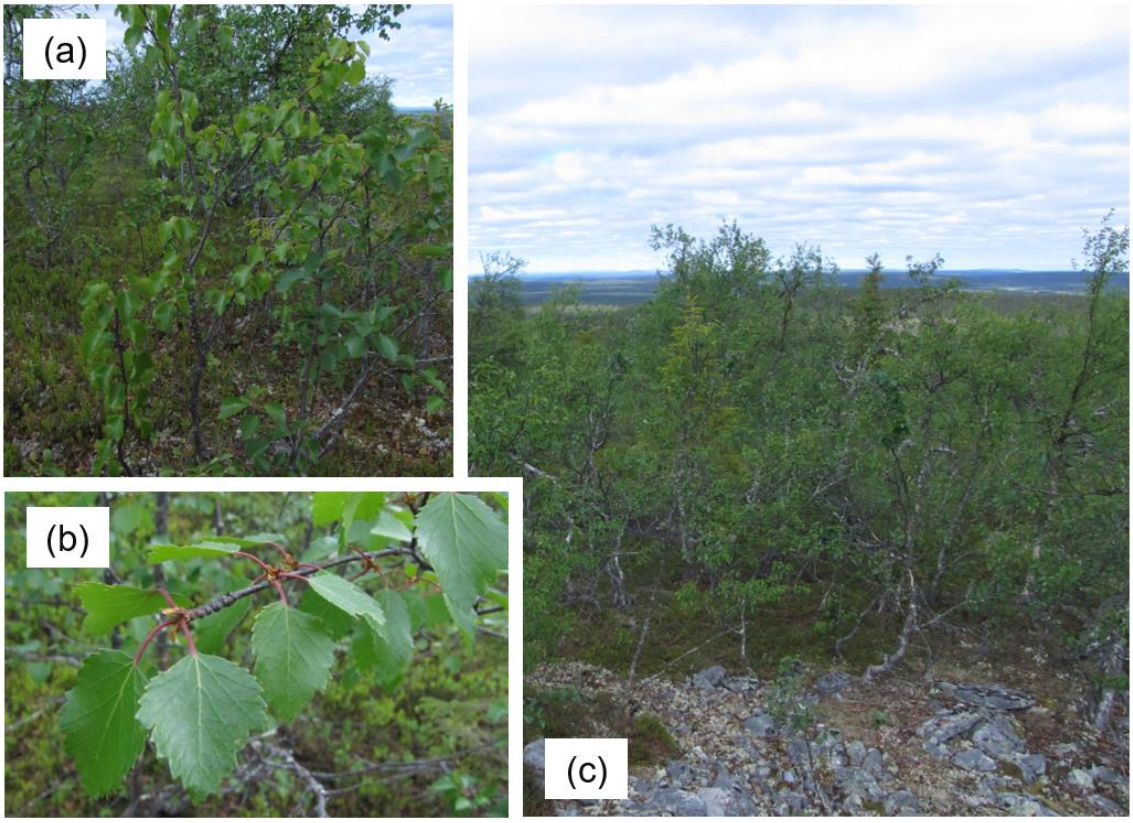


Fig 3. Mountain birch dominated forest on the north-facing slope of Värriö I fell: small mountain birch individual (a), closeup of leaves (b), and overview of the forest (c) (Karvinen 2020).

Geometrid moth outbreaks affect surface layer vegetation as well as trees (Tenow 1972 as cited by Jepsen 2013). Defoliation has an effect on below canopy light conditions, larvae droppings and pupae remains provide a nutrient boost to the ecosystem, and tree mortality can lead to decreased root competition (Jepsen et al. 2013; Karlsen et al. 2013). Both Jepsen et al. (2013) and Karlsen et al. (2013) reported the decrease of crowberry (*Empetrum nigrum ssp. hermaphroditum* L.) and an increase of wavy hair grass (*Deschampsia flexuosa* L.). Jepsen et al. (2013) added that the effect did not seem to be linear but exponential in a way that more severe moth damage resulted in a more profound shift in plant community. Karlsen et al. (2013) concluded that woody shrubs tolerate moth outbreaks in a similar fashion as mountain birches with several consequent years of defoliation leading to increased mortality.

Several studies have documented moth outbreak consequences for small rodents and ungulates (Jepsen et al. 2013), birds (Silvola 1967 as cited by Kallio and Lehtonen 1973; Vindstad et al. 2015) and saproxylic beetles (Vindstad et al. 2014). Severe moth outbreaks

and heavy defoliation can alter the state of the whole ecosystem. Still it is hard to say whether the changes will be permanent and irreversible. The changes in vegetation state following the geometrid outbreak of 2002-2008 in Norway reported by Jepsen et al. (2013) and Karlsen et al. (2013) are in keeping with earlier results by Kallio and Lehtonen (1973) on autumnal moth outbreak in Utsjoki 1965-66. Kallio and Lehtonen (1973) pointed out that woody shrubs had returned to areas that had experienced moth outbreaks even earlier in history. It is thus hard to determine the temporal scale of forest recovery, as the Varangerfjord studies (e.g. Jepsen et al. 2013 and Karlsen et al. 2013) had been conducted only a few years after the outbreak. Full recovery after severe defoliation has been estimated to take over 100 years (Bylund 1995 as cited by Bylund 1999).

Fig 4. Mountain birch forest of the fell slope shifts to coniferous dominance at lower altitudes on the east-facing slope of Värriö I (Karvinen 2020).

### 1.7 Research aims and hypotheses

Autumnal moth and winter moth are both quite intensively studied species and a lot is already known about their ecology. However, the majority of this research has concentrated on studying the behavior of only one of these species. Current climate-induced changes in the distribution of winter moth have raised the need for an integrated assessment of the two geometrid moths. This study aims to answer to that need.

The main aim of this research is to illustrate how autumnal moth and winter moth perform in relation to one another when they occur in same areas in northern and mountainous Fennoscandia. The aim is approached with the help of the following three research questions and hypotheses:

1) Do peak population densities of the two species temporally follow one another in turns or do they take place simultaneously in the same areas?

> **$H_0$**: Peak population densities of the two species do not occur simultaneously.
>
> **$H_1$**: Peak population densities take place simultaneously.

2) Is it possible to detect species specific distribution patterns based on elevation?

> **$H_0$**: There are species specific differences between the local distribution patterns based on elevation.
>
> **$H_1$**: No distribution differences regarding elevation can be observed.

3) How clear is the regulatory effect of winter temperature on population density fluctuations and are there differences between species in this regard?

> **$H_0$**: Winter temperature seems to be contributing to population dynamics of the species. There are also notable differences between the two species in this regard.
>
> **$H_1$**: Winter temperature cannot be treated as a major factor determining the population dynamics of the species.

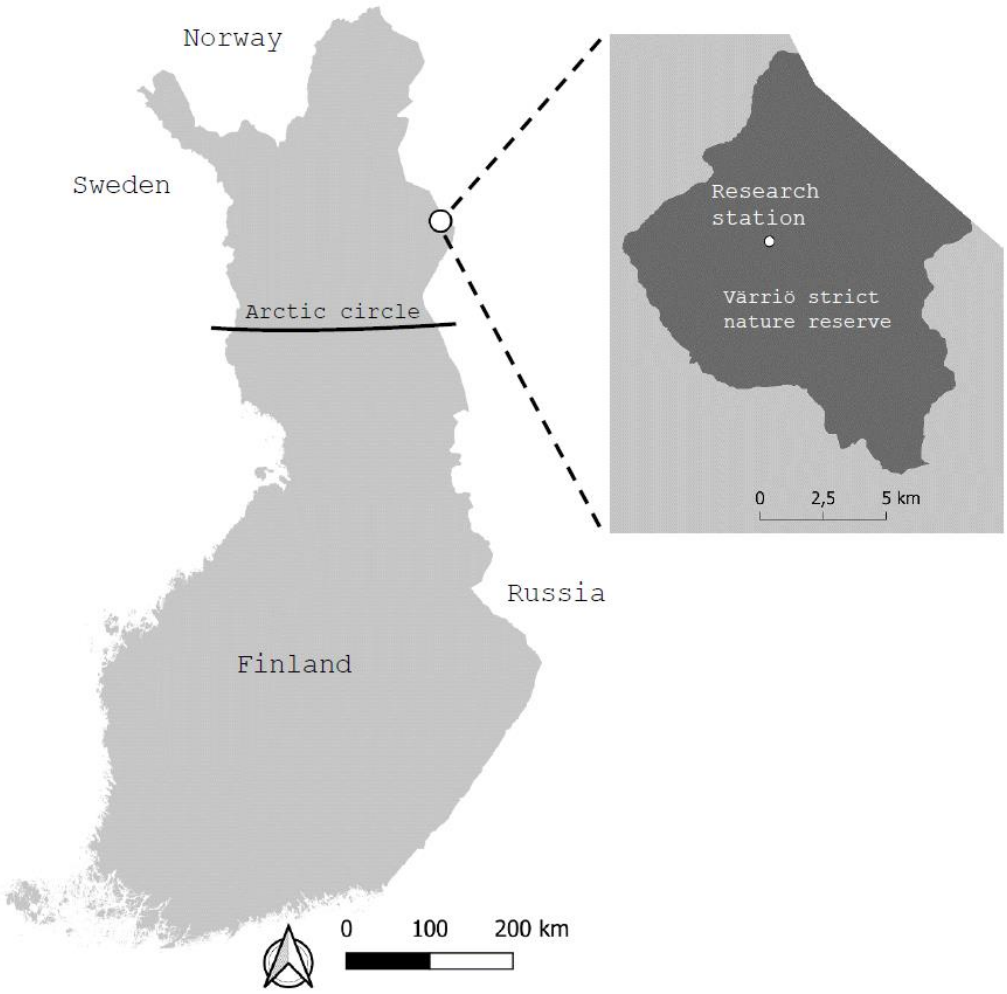


Fig 5. Värriö subarctic research station is located in Värriö strict nature reserve north of the arctic circle in Finnish Lapland (Karvinen 2020 based on maps by National Land Survey of Finland 2020b).

# 2. MATERIAL AND METHODS

## 2.1 Study site

Värriö subarctic research station (owned by University of Helsinki) was founded in 1967 with the purpose of studying natural ecosystems with long ecological time series (Hietajärvi 2017). The station is situated in Eastern Finnish Forest Lapland (67º 44’ N, 29º 37’ E) inside Värriö Strict Nature Reserve (Fig 5) roughly a hundred kilometers north of the Arctic circle (Pulliainen and Itämies 1988; Keret et al. 2020). The strict nature reserve was established in 1981 to ensure the preservation of natural habitats that could be used for research purposes (Hietajärvi 2017). The area is relatively far from any

permanent settlement and is characterized by low human impact on nature except for a tradition in reindeer husbandry (Keret et al. 2020). The station is located on the southern side of Kotovaara hill which is further followed south by Värriö fell range consisting of five fells named Ykkönen, Kakkonen, Kolmonen, Nelonen and Viitonen (translates to One, Two, Three, Four and Five). Snow-free period in the area last approximately from the end of May to mid-October and the annual precipitation is 595 mm on average (Keret et al. 2020). July is the warmest month and January the coldest with average temperatures of +13 ºC and -11,4 ºC, respectively (Keret et al. 2020). Continuous daylight period lasts from 30 May to 14 July (Keret et al. 2020).

## 2.2 Light trap time series

The first light trap to monitor nocturnal moths in Värriö was set up in 1976 (Itämies and Pulliainen 2006). In 1978 the number of traps was increased to 11 (Itämies and Pulliainen 2006) and the setup remained similar until 2010. After 2010 only two of the original traps (IDs two and five) remained in operation. The broad trap setup of 1978-2010 covered a range of different biotopes and altitudes beginning from the side of Kotovaara hill at 360,7 meters above sea level (m a.s.l.) and ending on top of the first Värriö fell (Ykkönen or Värriö I) at 473,3 m a.s.l. (Fig 6) (Pulliainen and Itämies 1988).

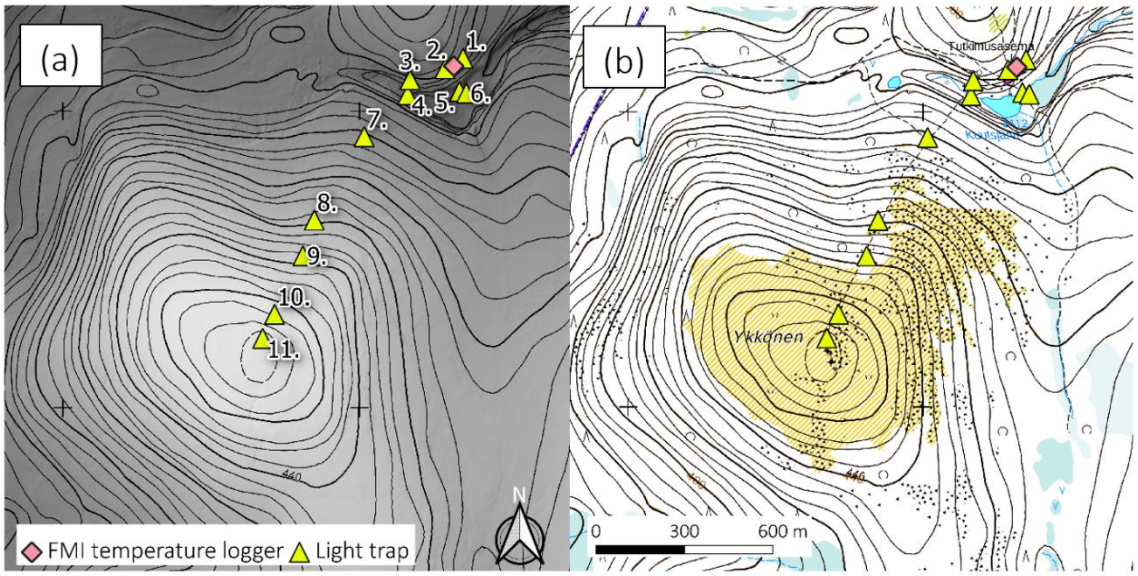


Fig 6. Light trap setup and the location of the Finnish Meteorological Institute's (FMI) temperature logger portrayed on hillshade relief (a) and basic map raster (b) (Karvinen 2020 based on maps by National Land Survey of Finland 2020b).

Light traps (model “Jalas” (Jalas 1960 as cited by Hunter et al. 2014)) (Fig 7) were operated on a yearly basis from mid-May to mid-October covering the whole snow free period in the area (e.g. Pulliainen and Itämies 1988; Itämies and Pulliainen 2006). During this period the 500 W blended light lamps were turned on daily from 8 PM to 8 AM (UTC+3) (Ylivinkka et al. 2020). Bright light would then attract insects that eventually ended up falling into the trap. The traps were situated in such way that almost no light from one trap intervened with the light of others after leaf out (Itämies and Pulliainen 2006). Daily catches were collected from all traps each morning and stored in freezer until the end of trapping season. After each season all macrolepidoptera species were identified and counted by Juhani Itämies. The whole 33-year-long time series totaled to 388 779 moth individuals of 456 species (Hunter et al. 2014). Even though Värriö area is not a real part of the outbreak range of either autumnal moth or winter moth, they do still occur in numbers large enough to make for an interesting assesment of their dynamics.

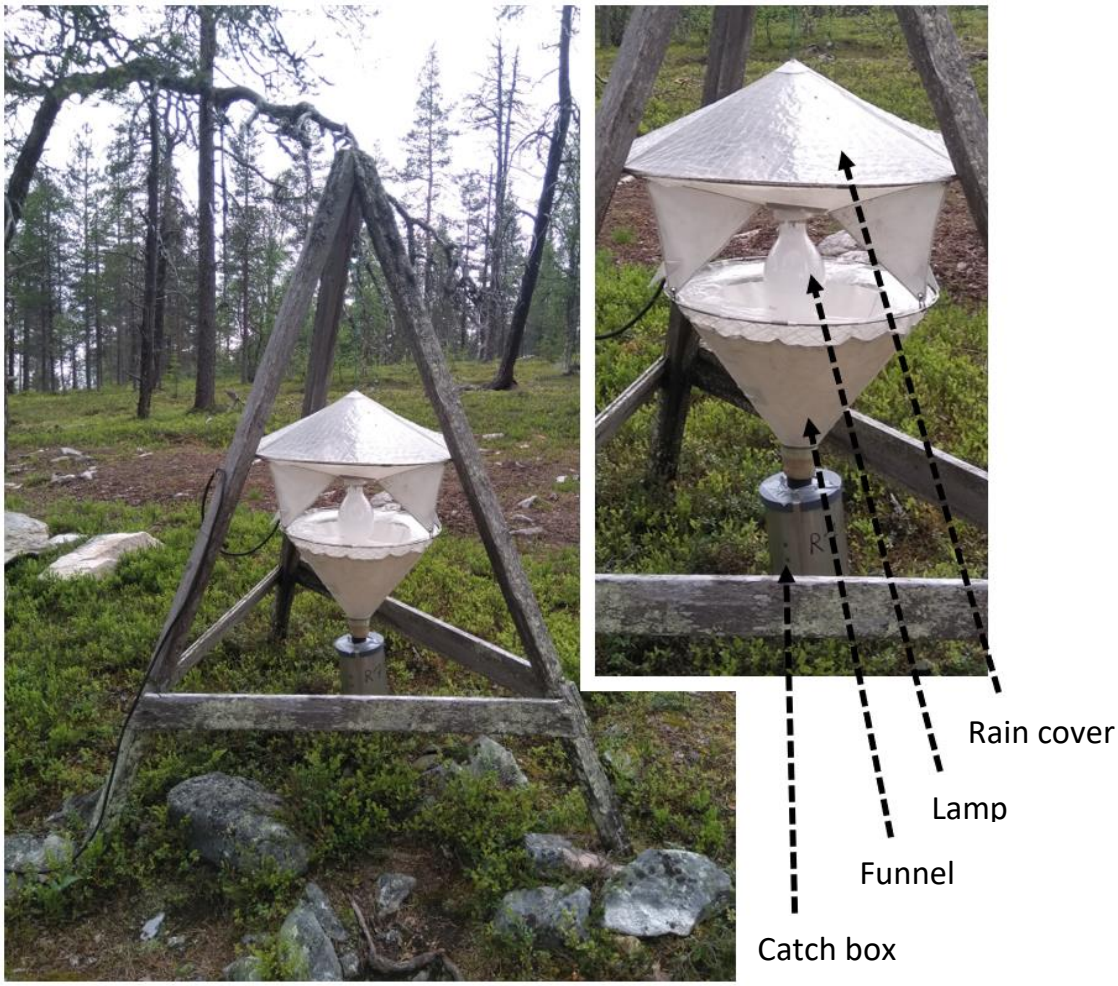


Fig 7. Light trap consists of rain cover, 500 W blended light lamp, funnel for falling insects, and catch box containing poison to kill the insects (Karvinen 2020 inspired by Ylivinkka et al. 2020).

Field study was conducted in the summer (June-July) of 2020 in order to get up-to-date and accurate measures of the habitats around the light trap locations (Table 1). All traps were located on site with Trimble GeoExplorer® 2008 series handheld GPS device (Trimble 2009) to obtain the coordinates. A differential correction was later applied to the location data based on the nearest GPSNet.fi reference station at Savukoski, 79 km away from the recorded location points. An accuracy of 1-2 meters was acchieved for 90 % of the location points after the correction. Trap elevations are derived from the Digital Elevation Model (DEM) by the National Land Survey of Finland (2020b). All GIS analyses were performed with QGIS (QGIS 2020).

Table 1. Background habitat data on the light trap locations obtained from a field study in 2020.

| Trap ID | Elevation (m a.s.l.) | Coordinates EUREF-FIN (X, Y) | Number of stems (n/ha) | *Dominating species* Tree layer | Field layer | Ground layer |
|---|---|---|---|---|---|---|
| 1 | 360,7 | 610350, 7517178 | 326 | PS (59%), BP (29%) | EN (43%), VM (29%) | DI (27%), PL (21%) |
| 2 | 364,9 | 610288, 7517143 | 247 | PS (84%), BP (10%) | VM (29%), EN (27%) | PL (49%), DI (10%) |
| 3 | 361,2 | 610171, 7517106 | 1814 | PS (88%), PT (7%) | EN (54%), VM (26%) | PL (64%), DI (1%) |
| 4 | 346,1 | 610163, 7517055 | 3406 | BP (47%), SS (22%) | VM (45%), CS (36%) | HY (20%), SP (19%) |
| 5 | 342,2 | 610338, 7517066 | 3247 | BP (61%), SS (17%) | VM (21%), TE (17%) | SP (19%), HY (14%) |
| 6 | 342,2 | 610361, 7517060 | 4074 | BP (82%), PA (10%) | VV (30%), TE (10%) | HY (11%), SP (8%) |
| 7 | 379,3 | 610016, 7516914 | 2483 | BC (77%), PS (9%) | EN (50%), VM (24%) | PL (48%), DI (33%) |
| 8 | 414,8 | 609848, 7516632 | 3756 | BC (74%), PA (23%) | EN (63%), VM (53%) | PL (54%), DI (18%) |
| 9 | 434,3 | 609809, 7516512 | 3342 | BC (78%), JC (12%) | EN (48%), VM (39%) | PL (55%), DI (34%) |
| 10 | 466,4 | 609714, 7516315 | 88 | BC (36%), JC (36%) | EN (34%), AU (11%) | DI (16%), CC (9%) |
| 11 | 473,3 | 609674, 7516234 | 40 | PS (60%), PA (40%) | EN (53%), AU (20%) | DI (14%), CC (12%) |

*AU = Arctostaphylos uva-ursi, BC = Betula pubescens subsp. czerepanovii, BP = Betula pubescens, CC = Cladonia subg. Cladina sp., CS = Cornus suecica, DI = Dicranaceae sp., EN = Empetrum nigrum subsp. hermaphroditum, HY = Hylocomiaceae sp., JC = Juniperus communis, PL = Pleurozium schreberi, PS = Pinus sylvestris, PT = Populus tremula, SP = Sphagnum sp., SS = Salix sp., TE = Trientalis europaea, VM = Vaccinium myrtillus, VV = Vaccinium vitis-idaea*

There has been vegetation analyses conducted around the trap locations in the past, most notably by Pulliainen and Itämies (1988). According to them (e.g. Itämies and Pulliainen 2006), traps 1-3 were located in sparse old-growth pine forest, 4-6 at the bottom of a canyon between Kotovaara and Värriö I dominated by spruce, 7-9 in mountain birch dominated forest belt and 10-11 in treeless fell top. A new analysis of tree layer, field layer, and ground layer vegetation was carried out in 2020 (Table 1). All individual trees (height > 50 cm) within a radius of 10 or 20 meters from light traps were identified and counted. Plot radius was determined by on-site estimation of tree density of the area with sparse areas (traps 1, 2, 10, and 11) being counted with 20 m radius. Field layer and ground layer vegetation was analysed by setting up four plots (1m x 1m) for each light trap (Fig 8). Some plots had to be moved from their original schematic positions because of poor representation of the habitat structure (i.e. human influence, paths). All plants within the plots were identified (up to species level in many cases) and their proportional coverage of the plot was estimated by eye. Percentages of the dominating field and ground layer species refer to their percentual coverage of the plot (average of all four plots per trap, accuracy of 1 %). Percentages of the dominating tree species illustrate the relative number of individuals of a single species compared to all species counted on that plot (accuracy of 1 %).

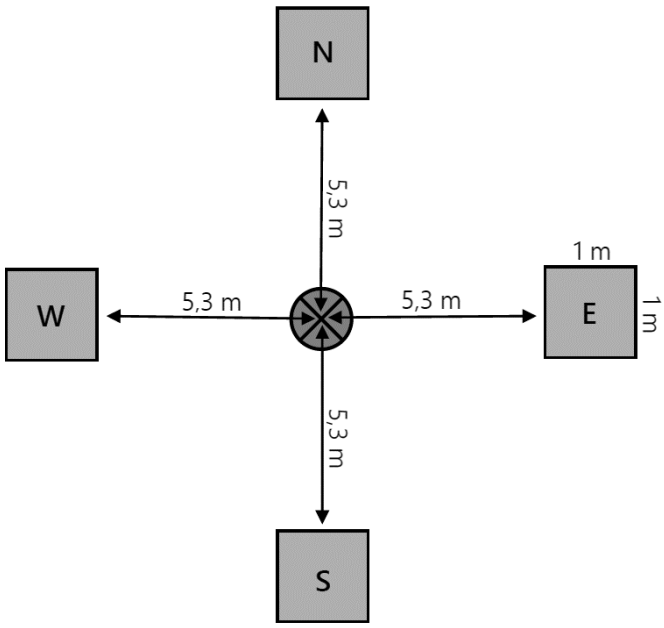


Fig 8. Setup for analyzing field and ground layer vegetation with four square plots centered around the light trap in all main cardinal directions (Karvinen 2020).

### 2.3 Temperature time series

Finnish Meteorological Institute (FMI) established a continuously operative weather observation station at Värriö research station in 1971 (FMI 2020a). Research station staff would at first conduct manual measurements twice a day, but these were later replaced by automated observation equipment in 1990s (Keret et al. 2020). The weather station is situated at an open area in a sparse pine forest at the lower south facing slope of Kotovaara hill (FMI 2020a). The location is 360 m a.s.l. (FMI 2020a) and some 25 meters east from the research station itself.

The station records numerous weather variables of which this study utilizes daily minimum and maximum temperatures and monthly mean temperature. Daily minimum and maximum temperatures are defined as the lowest and highest temperatures recorded in the period from 8 PM (9 PM in daylight saving time) the previous night to 8 PM (9 PM in daylight saving time) the current night (UTC+3) (FMI 2020b). Monthly mean temperature is the average of daily mean temperatures for that month (FMI 2020b). The data is available in the download service of FMI with CC BY 4.0 license (FMI 2020c). Four values were missing from the monthly mean temperature dataset. These were substituted with the average of minimum and maximum temperature readings for the specific months.

All daily temperature data was transformed to monthly variables in order to fit them into the analysis. Months from October to April were selected to investigate the development of cold season temperature variables and their potential effects on insect catch numbers. Monthly variables calculated for each of the seven months included:

1) Monthly mean temperature (see above for definition),

2) Mean on daily maximum temperatures,

3) Mean of daily minimum temperatures,

4) The highest daily maximum temperature,

5) The highest daily minimum temperature,

6) The lowest daily maximum temperature, and

7) The lowest daily minimum temperature.

Temperature dataset was also used to calculate the number of days (within one month) that fulfilled certain criteria. This was done to represent and assess the importance of the duration of cold spells when considering winter mortality of insect eggs. Criteria included the following:

1) Daily mean temperature < -10°C,

2) Daily mean temperature < -15°C,

3) Daily mean temperature < -20°C,

4) Daily mean temperature < -25°C,

5) Daily minimum temperature < -20°C,

6) Daily minimum temperature < -25°C,

7) Daily minimum temperature < -28°C, and

8) Daily minimum temperature < -35°C.

The calculated variables totaled to 15 per each of the seven studied months. These were converted into a year-based format to match the formatting of the light trap time series. The final temperature time series included a total of 105 variables for each of the years 1978-2010. As temperatures of a cold season affect insect populations in the following warm season, the monthly variables of the time series are paired with the insect catch numbers accordingly when analyzing their potential effects on the population dynamics. For example, winter moth catch numbers from 1996 are paired with temperature variables from October-December 1995 and January-April 1996.

### 2.4 Time series analysis

Insect occurrence data and temperature data are time series data by nature as they both have an integrated temporal ordering that is essential when conducting analyses on them (Woolridge 2003). Such data consists of single observations / cases that are related to each other, i.e. the time factor acts as a predictor of the dependent variable in a model (Smart Vision Europe 2020). This kind of data demands specifically suited statistical analyses (e.g. Stock and Watson 2015), as many of the data quality requirements of

traditional analysis methods are not met (e.g. the significance of the temporal ordering suppresses the often presumed randomness of cases / single observations). All statistical analyses in this study were conducted with Microsoft Excel (Microsoft 2020) and SPSS (IBM 2020).

Pearson correlation (McDonald 2014) coefficients were calculated to reveal possible trends in both insect and temperature data based on Hunter et al. (2014). Insect occurrence data was (natural) log transformed prior to analysis in order to stabilize the variance of the data (Lütkepohl and Xu 2009). The procedure was similar to Hunter et al. (2014) with the equation

$$y = \log_e (x + 1) \quad (1),$$

where y is the annual catch after transformation and x the annual catch before transformation. Variation in species occurrence between years and traps was evaluated with coefficient of variation (McDonald 2014) following the equation

$$CV = S / M \quad (2),$$

where CV is coefficient of variation, S refers to standard deviation and M to mean (Glen 2020b). This metric allows for an easy comparison of two sets of variables with differences in magnitude, as autumnal moth occurs in number far greater than winter moth.

The effect of altitude on species occurrence was analyzed with Spearman's rank correlation coefficient (McDonald 2014) and non-parametric Kruskal-Wallis test (McDonald 2014) inspired by Kosunen et al. (2017). Spearman's rank correlation was used to test the correlation between trap elevation (as a continuous variable) and yearly catch totals of winter moth and autumnal moth on each trap. Kruskal-Wallis test was used to determine if the yearly catch totals differed significantly between the eleven traps.

Time series analysis methods were used with the Forecasting add-on module (IBM 2012) of SPSS. It features modeling tools aimed at time series analysis and forecasting. Autocorrelation within the time series of both species was analyzed with a method based on Hunter et al. (1997). The log transformed catch data described above was detrended with methods of Berryman (1994 as cited by Hunter et al 1997). Regression line was fitted through the data with equations

$$O(t) = 0{,}0783t - 152{,}98 \quad (3),$$

$$E(t) = -0{,}0829t + 172{,}83 \quad (4),$$

where t is the point in time. Equation 3 was used for winter moth and equation 4 for autumnal moth. Both time series were then separately transformed by

$$Y(t) = X(t) – P(t) + N \quad (5),$$

where Y(t) is the new, detrended time series, X(t) the untransformed time series, P(t) refers to the regression line of O(t) or E(t) depending on the species, and N the mean of the untransformed time series. Partial autocorrelation function (PACF) was generated with SPSS for both time series. The aim of autocorrelation analysis is to see whether current observations are influenced by past observations in such magnitude that needs to be taken into account in modeling procedures (DataJobs 2020). The analysis can also reveal evidence of density dependent factors operating on population fluctuations (Hunter et al. 1997).

Cross-correlation function (CCF) of SPSS was used to see whether the population peaks and drops of the two insect species are temporally synched. The original (untransformed in any way) catch data was automatically first differenced before applying the cross-correlation function. First differencing is a procedure of calculating differences among pairs of observations with a lag of one period (= year) in order to turn a nonstationary (trend is present) time series into stationary (no trend) (DataJobs 2020).

The last part of the analysis was to see whether some naturally varying temperature factors could be linked to changes in insect abundance over the course of the whole time series. This goal was approached with the Expert Modeler method of the Forecasting module. Expert modeler needs an input time series and a set of predictor variables to find a best-fitting model for the data (IBM 2011). It considers both exponential smoothing and ARIMA (p, d, q) (Auto Regressive Integrated Moving Average) models and transforms the data if needed with differencing and / or square root or natural log transformation (IBM 2011). ARIMA models are defined with components p (auto-regressive term), d (trend term), and q (moving average term). P describes the dependency (= auto-correlation) among successive observations, d defines the amount of differencing needed to make non-stationary time series stationary, and q determines the persistence of random shock from one observation to the next (DataJobs 2020). The Expert Modeler method can be used to find the statistically significant predictor variables from a large selection (IBM

2011). The insect time series data was not split into specific training and evaluating periods / datasets because of its relatively short 33-year timespan.

# 3. RESULTS

## 3.1 Light trap time series

Catches of autumnal moth and winter moth during the whole time series (Fig 9) totaled to 175 789 and 3811, respectively. Traps six, four, one and three accounted for the most catches of autumnal moth (in respective order) (Table 2). The same traps did account for the most catches of winter moth, but the order differed slightly. Kruskal-Wallis test revealed how yearly catch totals were significantly different between the eleven traps for both winter moth (H = 81,281 with p < 0,000 and df = 10) and autumnal moth (H = 170,459 with p < 0,000 and df = 10) (Table 2 and Fig 10).

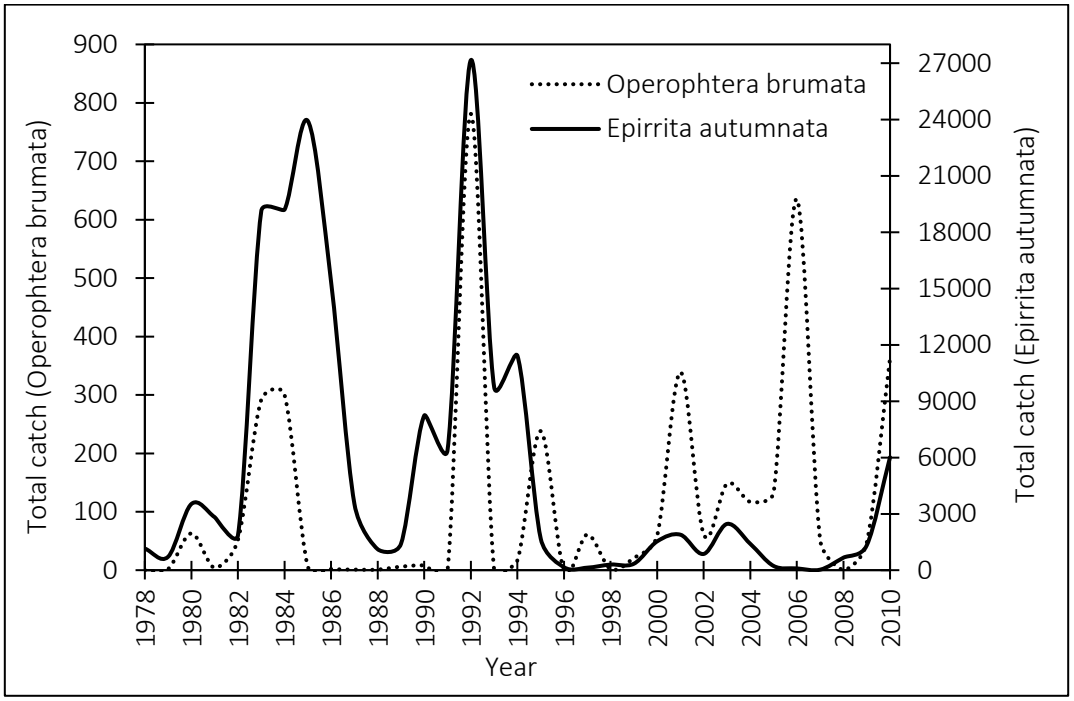


Fig 9. Total catches of autumnal moth and winter moth on separate axes throughout the whole time series (Karvinen2020).

There was more between-year variation in winter moth occurrence than in the occurrence of autumnal moth (Fig 11a), and both species exhibited more between-year variation in the traps located higher on the fell slope based on analysis with coefficient of variation (Table 2). Autumnal moth catches distributed more evenly across all traps whereas winter moth displayed more variation in the way with which its catches distributed across the traps on a single observation year (Fig 11b). The between-trap variation of winter moth did seem to be decreasing in the course of the time series. Spearman's rank correlation coefficient revealed statistically significant decrease in yearly catch totals for both winter moth ($r = -0{,}401$ with $p < 0{,}000$) and autumnal moth ($r = -0{,}548$ with $p < 0{,}000$) with increase in elevation.

Table 2. Summary of autumnal moth (EA) and winter moth (OB) catches on all light traps throughout 1978-2010.

| | | Trap ID | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
| **EA** | *Min* | 1 | 2 | 3 | 6 | 3 | 2 | 6 | 1 | 0 | 0 | 0 |
| | *Mean* | 816 | 455 | 806 | 861 | 406 | 952 | 762 | 192 | 64 | 4 | 9 |
| | *Max* | 5216 | 3199 | 4817 | 4056 | 2414 | 7388 | 3270 | 1059 | 369 | 59 | 223 |
| | *Var* | 1,66 | 1,56 | 1,38 | 1,35 | 1,54 | 1,71 | 1,26 | 1,25 | 1,18 | 2,58 | 4,18 |
| | *%* | 15,3 | 8,5 | 15,1 | 16,2 | 7,6 | 17,9 | 14,3 | 3,6 | 1,2 | 0,1 | 0,2 |
| | *K-WR* | 226,6 | 199,8 | 237,6 | 250,0 | 203,1 | 234,3 | 246,6 | 180,2 | 131,6 | 46,3 | 46,1 |
| | ***Total*** | 26917 | 15009 | 26590 | 28395 | 13408 | 31425 | 25143 | 6338 | 2126 | 135 | 303 |
| **OB** | *Min* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | *Mean* | 18 | 6 | 17 | 20 | 11 | 15 | 15 | 8 | 1 | 0 | 0 |
| | *Max* | 217 | 46 | 179 | 147 | 85 | 171 | 109 | 66 | 12 | 2 | 1 |
| | *Var* | 2,26 | 1,88 | 2,03 | 1,79 | 1,67 | 1,94 | 1,71 | 1,95 | 2,3 | 3,37 | 3,94 |
| | *%* | 15,6 | 5,2 | 15,1 | 17,1 | 9,9 | 15,6 | 13 | 7,3 | 1,1 | 0,1 | 0,1 |
| | *K-WR* | 217,3 | 181,6 | 217,0 | 225,1 | 205,6 | 220,5 | 220,2 | 181,3 | 136,5 | 100,6 | 96,5 |
| | ***Total*** | 595 | 197 | 574 | 650 | 378 | 595 | 494 | 280 | 42 | 4 | 2 |

*Min = minimum yearly catch, Mean = average yearly catch, Max = maximum yearly catch, Var = between-year coefficient of variation, % = percentage of the total catch, K-WR = Kruskal-Wallis test rank score (n = 33), Total = total number of catches in 1978-2010*

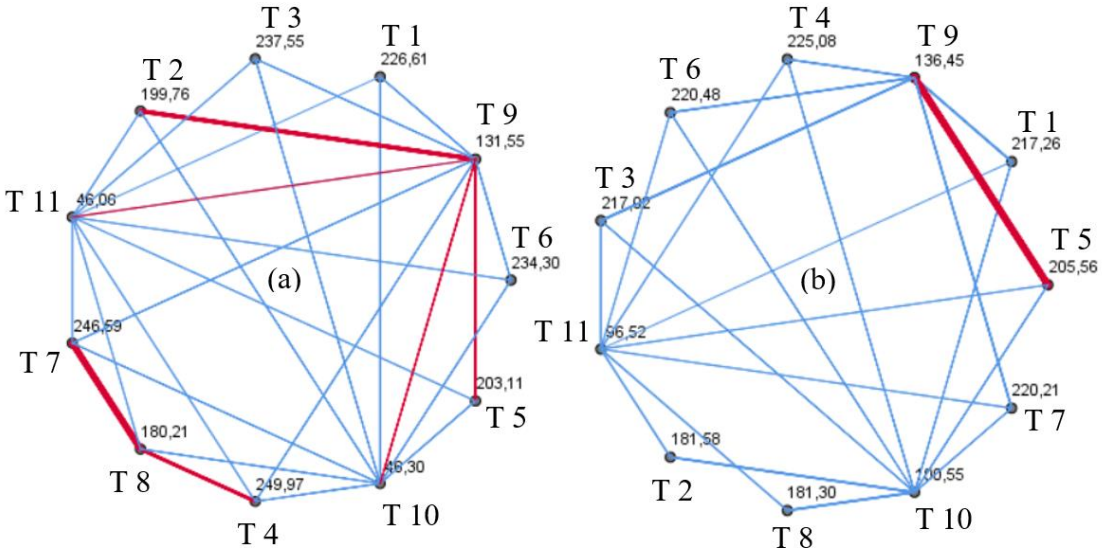


Fig 10. Pairwise comparison of trap catch totals with Kruskal-Wallis test highlights the significant differences (in red) for autumnal moth (a) and winter moth (b) (IBM 2020).

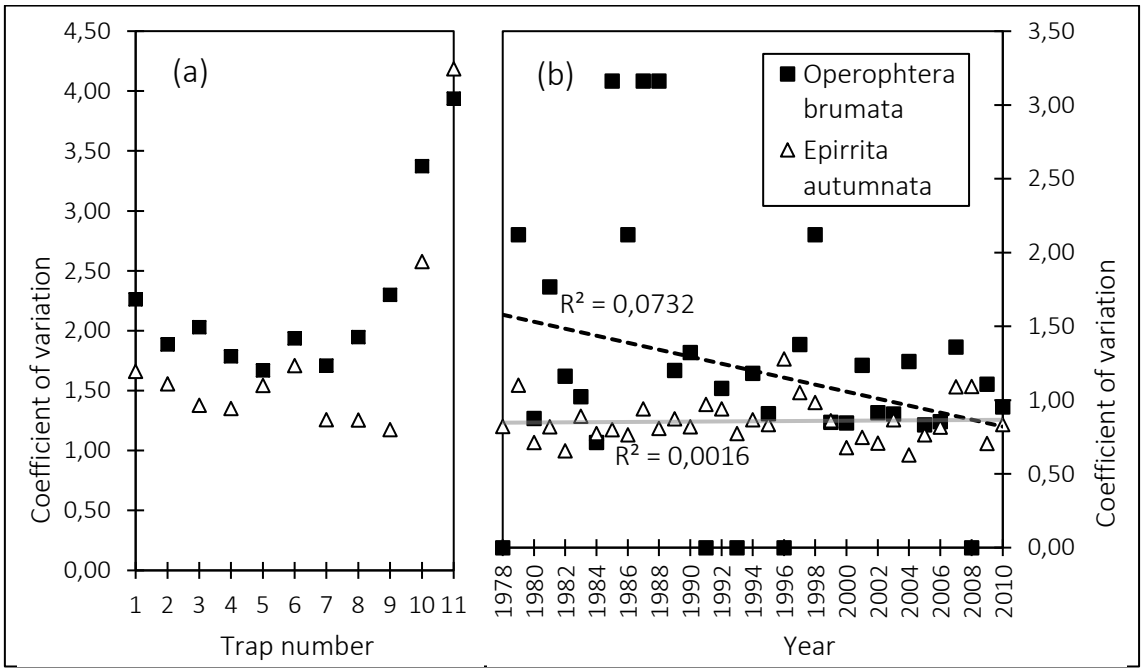


Fig 11. Coefficient of variation in moth catches when comparing trap results (a) and yearly totals (b). Dashed black line ($R^2$=0,0732) represents the trend in winter moth and solid gray line ($R^2$=0,0016) in autumnal moth. (Karvinen 2020).

Table 3. Pearson correlation coefficients revealed the trends in moth catch numbers both for yearly totals and separate traps (a). Development of yearly catch distribution (single traps share of the yearly total) is also presented (b). Significant correlations ($p < 0,05$) are in bold.

| | | *Winter moth* | | | *Autumnal moth* | | |
|---|---|---|---|---|---|---|---|
| | | Pearson correlation | Sig. (2-tailed) | N | Pearson correlation | Sig. (2-tailed) | N |
| **(a)** | Trap 1 | 0,255 | 0,152 | 33 | **-0,510** | **0,002** | 33 |
| | Trap 2 | 0,108 | 0,551 | 33 | **-0,535** | **0,001** | 33 |
| | Trap 3 | 0,329 | 0,062 | 33 | **-0,464** | **0,007** | 33 |
| | Trap 4 | **0,411** | **0,018** | 33 | **-0,527** | **0,002** | 33 |
| | Trap 5 | 0,278 | 0,117 | 33 | **-0,509** | **0,002** | 33 |
| | Trap 6 | 0,255 | 0,152 | 33 | **-0,515** | **0,002** | 33 |
| | Trap 7 | **0,528** | **0,002** | 33 | -0,334 | 0,057 | 33 |
| | Trap 8 | **0,359** | **0,040** | 33 | -0,126 | 0,485 | 33 |
| | Trap 9 | 0,305 | 0,084 | 33 | -0,109 | 0,546 | 33 |
| | Trap 10 | 0,300 | 0,090 | 33 | -0,296 | 0,095 | 33 |
| | Trap 11 | 0,093 | 0,605 | 33 | -0,254 | 0,154 | 33 |
| | Total | **0,348** | **0,047** | 33 | **-0,466** | **0,006** | 33 |
| **(b)** | Trap 1 | -0,128 | 0,478 | 33 | **-0,528** | **0,002** | 33 |
| | Trap 2 | -0,177 | 0,323 | 33 | **-0,500** | **0,003** | 33 |
| | Trap 3 | -0,088 | 0,626 | 33 | -0,166 | 0,355 | 33 |
| | Trap 4 | 0,190 | 0,290 | 33 | -0,143 | 0,429 | 33 |
| | Trap 5 | 0,101 | 0,576 | 33 | -0,238 | 0,183 | 33 |
| | Trap 6 | -0,118 | 0,513 | 33 | **-0,470** | **0,006** | 33 |
| | Trap 7 | 0,196 | 0,274 | 33 | **0,675** | **0,000** | 33 |
| | Trap 8 | **0,349** | **0,047** | 33 | **0,574** | **0,000** | 33 |
| | Trap 9 | -0,231 | 0,196 | 33 | **0,435** | **0,011** | 33 |
| | Trap 10 | 0,313 | 0,076 | 33 | -0,116 | 0,522 | 33 |
| | Trap 11 | 0,161 | 0,371 | 33 | -0,106 | 0,557 | 33 |

Pearson correlation coefficients summarize the trends in moth catches (Table 3). Section (a) depicts the change in actual catch numbers whereas section (b) considers the changes in the distribution of yearly catch total across all traps. Total catches of autumnal moth experienced a significant (two-tailed test, $p < 0,05$) decline whereas winter moth catches had an increasing trend. Autumnal moth catches on single traps showed significant decline in traps one to six. Winter moth experienced significant increase in traps four, seven and eight. The distribution of winter moth catches across eleven traps had remained somewhat steady except for the significant increase in the share of trap 9. The yearly

distribution of autumnal moth had experienced more profound shifts as traps one, two and six presented a significant decline in importance with a simultaneous increase in the share of traps seven, eight and nine.

Partial autocorrelation function (Fig 12) illustrated how autumnal moth population possessed strong autocorrelation with a lag value of one year. The autocorrelation in winter moth population did not reach significant levels (= exceed 95 % confidence limits). Cross-correlation function (Fig 13) revealed a significant correlation between catch totals of the two species only at lag value zero.

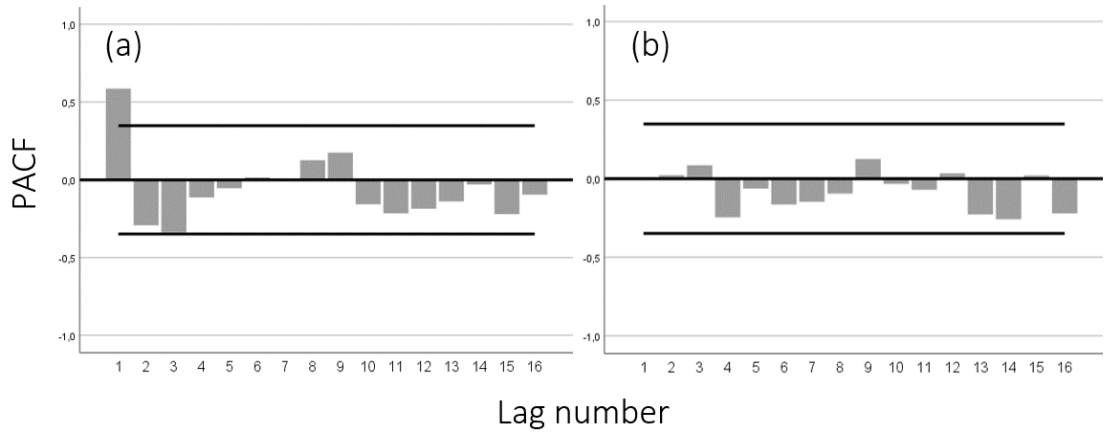


Fig 12. Partial autocorrelation function (PACF) for autumnal moth (a) and winter moth (b). Gray bars illustrate the amount of correlation and black lines are 95 % confidence limits (IBM 2020).

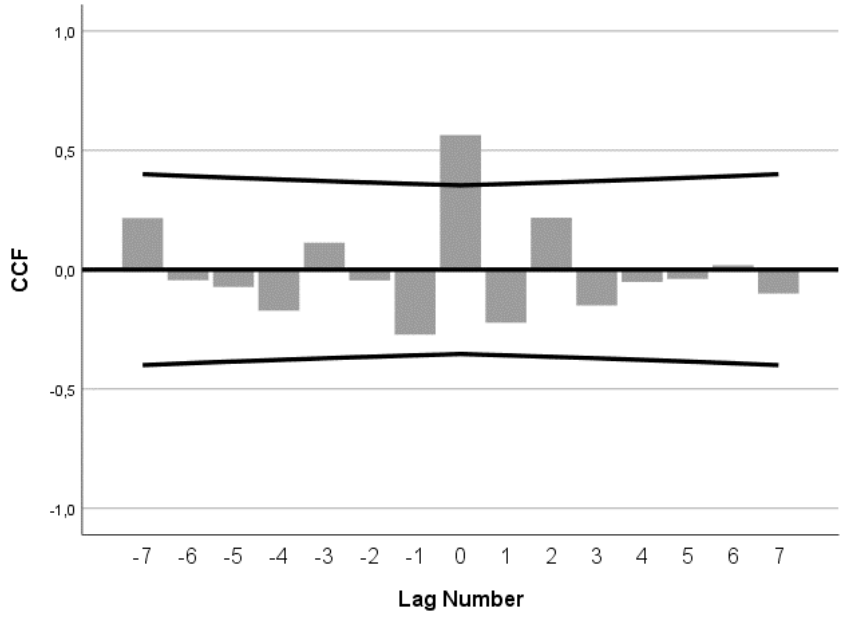


Fig 13. Cross-correlation function (CCF) between winter moth and autumnal moth catch numbers. Gray bars illustrate to the amount of correlation and black lines are 95 % confidence limits (IBM 2020).

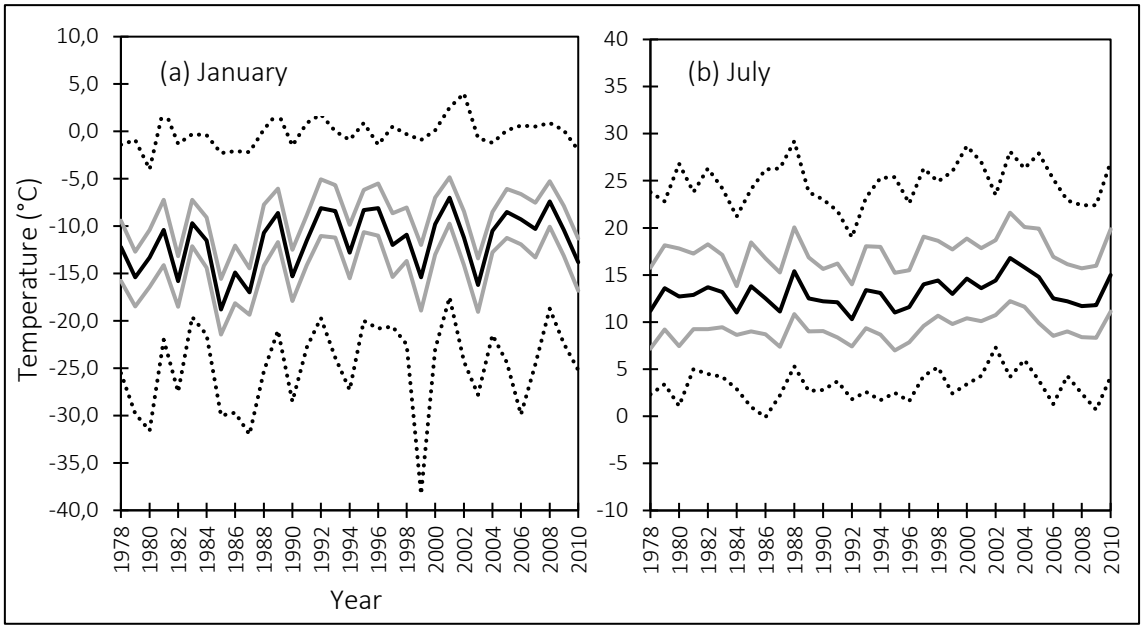


Fig 14. Temperature of the coldest month January (a) and the warmest month July (b). Black line represents monthly mean temperature, gray lines averages of daily minimum and maximum temperatures during the month, and dashed lines the absolute maximum and minimum daily temperatures during the month. (Karvinen 2020).

### 3.2 Temperature time series

Temperature data from the warmest and coldest months (Fig 14) demonstrated how there was more variation in daily temperatures in summer than in winter and how the absolute minimum temperatures in January fluctuated the most of the parameters displayed in the graph. Pearson correlation coefficients (Table 4) revealed a significant (two-tailed test, N=32 $p < 0,05$) increase in the monthly mean temperature of December and January. The most notable difference between the two months was that the absolute daily minimum temperature (min of min) and the lowest daily maximum temperature (min of max) during the month did not feature a significant increase in January as they did in December. Highest daily maximum temperature (max of max) was significantly increasing also in March and April. Highest daily minimum temperatures (max of min) were increasing in November and April. Lowest daily maximum temperature (min of max) featured a significant increase in November. Monthly mean temperature of July (not presented in Table 4) was not significantly increasing ($r = 0,233$ and Sig. = 0,200).

Table 4. Pearson correlation coefficients reveal the trends in temperature between 1978 and 2009. Significant correlations (2-tailed test, N = 32, p < 0,05) are in bold. Paired numbers represent the correlation coefficient (upper) and its significance (lower).

| | October | November | December | January | February | March | April |
|---|---|---|---|---|---|---|---|
| *Mean* | 0,190<br>0,298 | 0,313<br>0,081 | **0,455**<br>**0,009** | **0,421**<br>**0,016** | 0,097<br>0,599 | 0,138<br>0,452 | 0,252<br>0,164 |
| *Mean of max* | 0,201<br>0,271 | 0,297<br>0,098 | **0,469**<br>**0,007** | **0,408**<br>**0,020** | 0,121<br>0,511 | 0,237<br>0,191 | 0,337<br>0,059 |
| *Mean of min* | 0,206<br>0,257 | 0,348<br>0,051 | **0,457**<br>**0,008** | **0,450**<br>**0,010** | 0,119<br>0,516 | 0,098<br>0,595 | 0,233<br>0,200 |
| *Max of max* | 0,072<br>0,696 | 0,099<br>0,591 | **0,412**<br>**0,019** | **0,373**<br>**0,035** | 0,079<br>0,666 | **0,397**<br>**0,025** | **0,412**<br>**0,019** |
| *Max of min* | -0,030<br>0,871 | **0,374**<br>**0,035** | **0,356**<br>**0,045** | **0,434**<br>**0,013** | 0,036<br>0,846 | 0,343<br>0,055 | **0,391**<br>**0,027** |
| *Min of max* | 0,322<br>0,072 | **0,455**<br>**0,009** | **0,422**<br>**0,016** | 0,277<br>0,125 | 0,125<br>0,496 | 0,170<br>0,353 | 0,031<br>0,867 |
| *Min of min* | 0,245<br>0,176 | 0,301<br>0,094 | **0,372**<br>**0,036** | 0,228<br>0,209 | 0,043<br>0,816 | 0,112<br>0,543 | 0,014<br>0,940 |

The number of days with a mean temperature below -15°C was significantly (two-tailed test, N=32 p < 0,05) decreasing in December and January (Table 5). Increasing the threshold criteria limit of mean temperature to below -20°C still showed a significant decline in December but also in November. The number of days with a minimum temperature below -20°C was also significantly decreasing in December. Nearly all other criteria resulted in decreasing trends that were not statistically significant. The number of days with a minimum temperature below -35°C was not analyzed because of their too sparse occurrence in the dataset.

### 3.3 Observed effects of temperature on population dynamics

SPSS Expert Modeler could not find any statistically significant predictor variables to explain variation in autumnal moth catch numbers. Hence, three models were created to assess the possible connections of temperature variables on the development of winter moth populations. All models were ARIMA (0,0,0) models.

Table 5. Pearson correlation coefficients reveal the trends in the number of days that meet certain temperature criteria each month between 1978 and 2009. Significant correlations (2-tailed test, N = 32, p < 0,05) are in bold. Paired numbers represent the correlation coefficient (upper) and its significance (lower). All conditions were not met for all months.

| | October | November | December | January | February | March | April |
|---|---|---|---|---|---|---|---|
| *Mean* | -0,114 | -0,318 | **-0,496** | **-0,499** | -0,162 | -0,186 | -0,232 |
| *< -10°C* | 0,534 | 0,077 | **0,004** | **0,004** | 0,377 | 0,308 | 0,202 |
| *Mean* | - | -0,330 | **-0,446** | **-0,404** | -0,201 | -0,179 | - |
| *< -15°C* | | 0,065 | **0,011** | **0,022** | 0,270 | 0,327 | |
| *Mean* | - | **-0,375** | **-0,357** | -0,317 | -0,095 | -0,243 | - |
| *< -20°C* | | **0,035** | **0,045** | 0,077 | 0,605 | 0,180 | |
| *Mean* | - | - | - | -0,221 | -0,144 | - | - |
| *< -25°C* | | | | 0,224 | 0,433 | | |
| *Min* | - | -0,304 | **-0,387** | -0,347 | -0,113 | -0,133 | - |
| *< -20°C* | | 0,091 | **0,029** | 0,052 | 0,539 | 0,468 | |
| *Min* | - | -0,263 | -0,269 | -0,235 | -0,071 | -0,243 | - |
| *< -25°C* | | 0,146 | 0,136 | 0,195 | 0,700 | 0,180 | |
| *Min* | - | - | 0,165 | -0,130 | -0,067 | - | - |
| *< -28°C* | | | 0,366 | 0,479 | 0,717 | | |

Table 6. Comparison of the characteristics and fit statistics of three models M1 (all variables as input), M2 (only temperature values as input), and M3 (only criteria days as input).

| | | *Model fit statistics* | | | *Ljung - Box Q(18)* | | | |
|---|---|---|---|---|---|---|---|---|
| Model | Predictors (n) | R-Squared | RMSE | Normalized BIC | Statistics | DF | Sig. | OL (n) |
| M1 | 6 | 0,937 | 56,592 | 9,155 | 18,070 | 18 | 0,451 | 2 |
| M2 | 3 | 0,858 | 79,479 | 9,509 | 20,950 | 18 | 0,282 | 2 |
| M3 | 3 | 0,838 | 99,335 | 10,557 | 23,869 | 18 | 0,159 | 1 |

*Normalized BIC = Normalized Bayesian Information Criteria, OL = Number of automatically detected outliers, RMSE = Root Mean Square Error*

First model on winter moth (M1) included an input of all 105 temperature variables as predictors, the second model (M2) included only the variables that are absolute temperature values by nature (n = 49), and the third model (M3) included the variables that were the numbers of days fulfilling certain criteria (n = 56). This was done to study the effects of single cold events and the duration of cold spells both separately and in interaction. Table 6 presented goodness-of-fit statistics for all three models and Fig 15 illustrated graphically how the models were able to capture the details of the original time series.

Expert Modeler analyzed the input of predictor variables and formed a model that contained the statistically significant ones (Table 7). This procedure resulted in M1 containing six predictors while M2 and M3 both contained three. All goodness-of-fit statistics refer to M1 as being the most comprehensive and explanatory model. Significance of the Ljung-Box (or modified Box-Pierce) statistic was larger than 0,05 which implied that all of the models are correctly specified. A significance value less than 0,05 would imply the model cannot account for some structure observed in the original time series (IBM 2011). Expert Modeler automatically detected potential outliers (OL in Table 6) and modeled them appropriately without the need to remove them from the time series (IBM 2011).

Predictor variables were treated as numerators (N) or denominators (D). Numerators took into account the predictor variable values per se, whereas denominators considered deviations from the series mean of the predictor variable when predicting current values of the dependent series (IBM 2011). Predictor variables were also considered with various lags. A lag value of zero implied that predictor variable values at time t are used to predict the values of dependent time series at time t. Increasing the lag value increases the number of steps taken back in time in the predictor time series; A lag value of 1 implied that predictor variable values at time t and t-1 were used to predict values of the dependent time series at time t. Some predictor variables were also considered to affect the dependent variable only with a delay (DL).

Model one considers absolute minimum temperature of April as the most significant predictor of winter moth catch numbers followed by a variable describing November temperatures. Model two puts the most emphasis on April minimum temperatures whereas model three again emphasizes November. The lowest temperatures of January

are referred to by models one and three. Model one also features the lowest temperatures of December and the highest minimum temperatures of March.

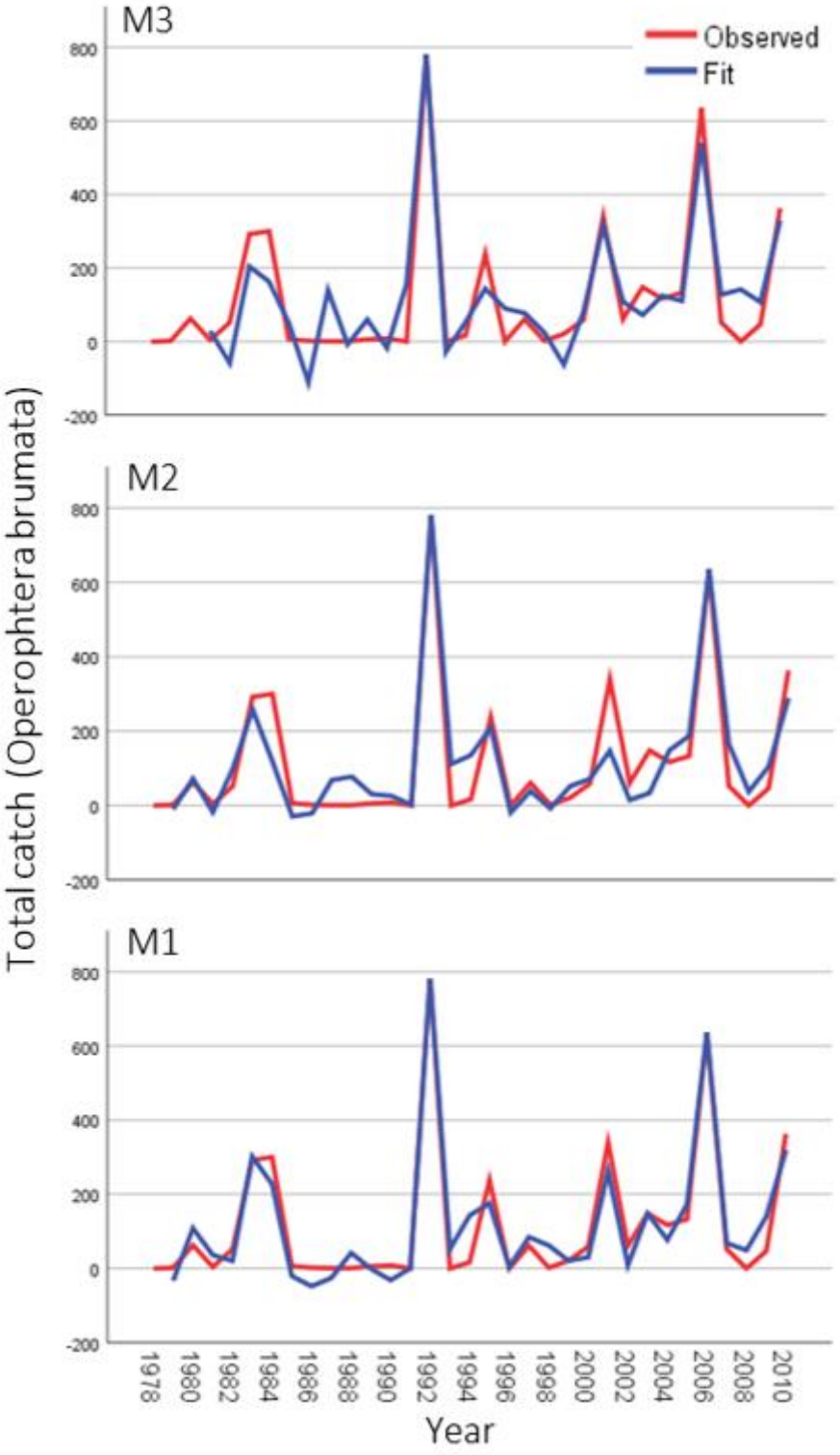


Fig 15. Graphical output of Expert Modeler demonstrates the performance of the three models compared to the original time series of winter moth catch numbers (IBM 2020).

Table 7. Automatically selected predictor variables of the three models M1, M2, and M3.

| Model | Variable | | Lag | Estimate | SE | t | Sig. |
|---|---|---|---|---|---|---|---|
| **M1** | OB total | C | | 572,242 | 91,792 | 6,234 | 0,000 |
| | Jan. min of min | N | Lag 0 | 8,271 | 2,847 | 2,905 | 0,008 |
| | Apr. min of min | N | Lag 0 | 16,725 | 4,074 | 4,106 | 0,000 |
| | Mar. max of min | N | Lag 0 | -20,870 | 6,052 | -3,448 | 0,002 |
| | Jan. days min < -35 | N | Lag 0 | 78,084 | 36,781 | 2,123 | 0,045 |
| | Dec. days min < -28 | N | Lag 0 | 163,622 | 59,068 | 2,770 | 0,011 |
| | Nov. days mean < -10 | N | Lag 0 | -7,152 | 2,010 | -3,558 | 0,002 |
| | | | Lag 1 | 6,311 | 2,122 | 2,974 | 0,007 |
| **M2** | OB total | C | | 749,671 | 120,174 | 6,238 | 0,000 |
| | Apr. min of min | N | Lag 0 | 23,418 | 5,424 | 4,318 | 0,000 |
| | Nov. max of max | DL | | 1 | | | |
| | | N | Lag 0 | -17,069 | 7,846 | -2,176 | 0,039 |
| | Nov. mean of min | N | Lag 0 | 13,661 | 5,594 | 2,442 | 0,022 |
| | | | Lag 1 | -20,335 | 6,191 | -3,284 | 0,003 |
| **M3** | OB total | C | | 306,612 | 51,489 | 5,955 | 0,000 |
| | Jan. days mean < -25 | N | Lag 0 | -144,843 | 39,308 | -3,685 | 0,002 |
| | | | Lag 1 | -119,798 | 33,722 | -3,552 | 0,002 |
| | | D | Lag 1 | 0,939 | 0,160 | 5,853 | 0,000 |
| | | | Lag 2 | -0,305 | 0,094 | -3,246 | 0,004 |
| | Jan. days min < -28 | N | Lag 0 | 104,999 | 33,939 | 3,094 | 0,006 |
| | | | Lag 3 | 38,837 | 13,924 | 2,789 | 0,012 |
| | Nov. days mean < -10 | N | Lag 0 | -17,355 | 3,907 | -4,442 | 0,000 |
| | | | Lag 1 | 11,068 | 3,180 | 3,481 | 0,003 |
| | | | Lag 2 | 16,730 | 4,220 | 3,964 | 0,001 |
| | | D | Lag 2 | -0,676 | 0,144 | -4,691 | 0,000 |

*C = Constant, D = Denominator, DL = Delay, N = Numerator, SE = Standard Error*

# 4. DISCUSSION

## 4.1 Peak population densities

The rather synchronous population development of the two species can be seen even based on simple plotting of the catch totals (Fig 9). This is further proved to be statistically significant by the strong cross-correlation observed in CCF (Fig 13). The strength of correlation exceeded 95 % confidence limits only at lag value zero. It implies that the two species fluctuated synchronously but were not actually affected by the population densities of each other. Would the strongest correlation appear with a lag value other than zero, it could be interpreted as one species affecting the other by its presence. Currently, the best interpretation is that both species were reacting simultaneously and similarly to fluctuations in some other environmental factor(s).

Because of their similar niches, it would be tempting to assume there to be some sort of notable effects of resource competition, which would in turn lead to asynchrony in population peaks. However, as the catch totals of winter moth and autumnal moth (Table 2) were so remarkably different in magnitude, the effect of inter-species competition is not likely present. Such conclusion is supported by Ammunét et al. (2010) who concluded that inter-specific competition is not capable of creating time-lags between population cycles or hindering the range expansion of winter moth. Still, time-lags in population peaks have been reported by e.g. Tenow et al. (2007) and Jepsen et al. (2013). Such time-lags can thus exist as a result of something else than direct or indirect resource competition between autumnal moth and winter moth. Tenow et al. (2007) did also point out how the population fluctuations were more synchronous, when overall population densities were low. This remark is well in keeping with the results of this current study, as Värriö does not currently belong to the geographical range experiencing the most numerous population densities.

Results of the partial autocorrelation (PACF) analysis revealed how both species fluctuated in roughly seven-year cycles (Fig 12). However, it needs to be acknowledged how population fluctuations take place in less regular intervals at climatically continental areas such as Värriö (Niemelä and Neuvonen 1983 as cited by Virtanen et al. 1998; Ruohomäki et al. 1997 as cited by Virtanen et al. 1998). Therefore this result should only

be used to describe the fluctuation dynamics in this particular location and not applied to other areas. Cycle duration will likely have altered during the time series and be further altered in the future as the environmental conditions change.

### 4.2 Spatial distribution of the species

Both species decreased in abundance with an increase in trap elevation. Some sort of a trend was expected to be found since many of the environmental factors shaping the local species communities are affected by elevation (e.g. Hodkinson 2005). The trend was established in analysis that considered the whole light trap transect, not only the fell slope of Värriö I. Thus, the trend was at least similar enough (not to disturb the analysis) when ascending from traps four to six (the lowest points in the transect) to either traps seven to eleven (slope and top of Värriö I) or one to three (side of Kotovaara). The resulting trend, however, most likely represents for the most part the ascend to Värriö I, since the elevational gradient is much wider on that side of the transect. We can observe a sharp drop in catch numbers when ascending from trap seven to eight even by comparing catch totals of the whole time series (Table 2). This difference was most likely highlighted in the resulting overall trend of decline.

The yearly catch totals of autumnal moth featured a significant decline over the course of the whole time series whereas winter moth numbers possessed an increasing trend (Table 3a). The trends were somewhat different at different trap locations along the transect. The most significant increase of winter moth took place in traps four, seven, and eight. Traps seven to ten represent the actual mountain birch forest belt (Fig 16). Concurrently, autumnal moth decline was statistically significant in traps one to six, all of which are not located in mountain birch forest belt, or even on the actual fell slope. When analyzing the trends in the way yearly catches are distributed across all traps (Table 3b), the proportion of autumnal moth catches allocated in traps seven to nine was significantly increasing. Analysis with coefficient of variation (Table 2) also revealed how there was least year-to-year variation for autumnal moth occurrences in traps seven to nine. In conclusion, there seems to be a relatively stable autumnal moth population in the mountain birch belt. It is not as strongly a part of the overall decline of autumnal moth as is the case with the traps located outside of the fell range. When comparing the overall catch totals of each of the traps (Table 2), trap seven is the only one in the mountain birch belt representing more

than 10 % share of the total catch of all light traps in the whole time series. Thus, the declining overall trend is not surprising, even if the decrease in mountain birch belt is not as drastic.

Variation in yearly catch totals between the eleven traps was analyzed with coefficient of variation (Fig 11a). Winter moth occurrence had more year-to-year variation than autumnal moth in all traps besides trap eleven. Traps ten and eleven were located near the top of Värriö I and both of them had the most year-to-year variation in catch totals for both species. Especially winter moth seemed to exhibit more between-year variation in traps at higher altitudes as there was an increasing trend in coefficient of variation starting from trap seven. Traps one, three, four, six, and seven accounted for most of the catches of both species when analyzing the whole time series (Table 2). Coefficient of variation was also used to analyze how much the catch totals of the eleven traps differ from each other on a single year (Fig 11b). The differences between traps were greater for winter moth than for autumnal moth, even though the differences of winter moth occurrence seemed to have a decreasing trend. This could imply how some trap locations generally had a more stable, baseline population of both winter moth and autumnal moth while other traps could achieve larger yearly catch totals only at specific points of the overall population density fluctuation cycle operating on a larger areal basis. The way with which year-to-year variation in winter moth occurrence seemed to be stabilizing is well in accordance with the general increasing trend of the species.

### 4.3 Observed effects of temperature

The modeling approach utilized in the current study could only explain the development of winter moth catch numbers. This is likely due to the rather surprising declining trend present in autumnal moth catches, and possible limitations in the modeling practice itself. In any case, the development of winter moth population is probably the most interesting aspect to model considering the general viewpoints of this study. The aim to analyze the regulatory influence of single extreme cold events and cold spell durations with separate models did not produce expected results. While model M3 was supposed to highlight the effect of cold spell durations, it ended up emphasizing variables that describe the development of extreme minimum temperatures of January. Thus, the variables are discussed here in a way that summarizes all the models.

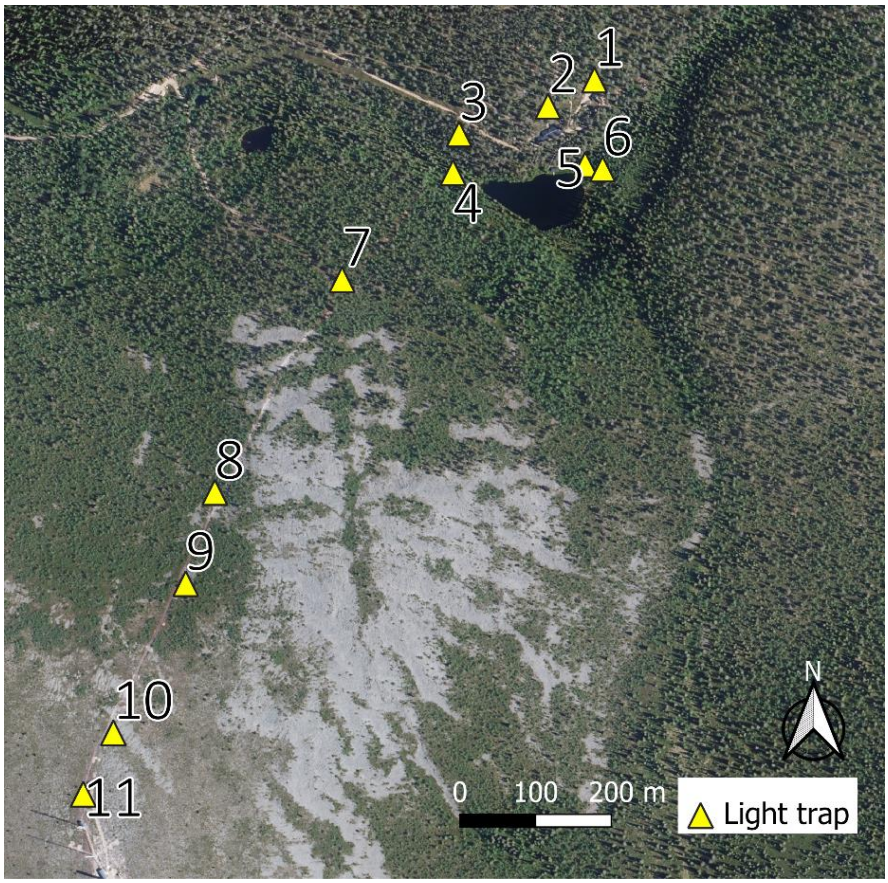


Fig 16. Light trap locations in orthophotography reveal features of the habitats surrounding them (Karvinen 2020 based on National Land Survey of Finland 2020b).

While all three models considered slightly different winter temperature variables to be of most regulatory significance (Table 7), model M1 did in fact quite nicely summarize the main features of the other two. It had the best statistics regarding its goodness-of-fit (Table 6) and it considered nearly all of its variables to have an effect with lag value 0. There is no point to consider other lag values as the cold season temperatures are presumed to affect only the insect population density during the subsequent warm season and not operate regulation over time-lags of multiple seasons or years.

All three models feature variables that clearly reflect on winter mortality of winter moth eggs. M1 included lowest daily minimum temperature of January as well as two variables depicting the number of extremely cold days in December and January. M3 also picked up the regulatory effect of minimum temperatures in January while simultaneously highlighting the temperatures of November. November temperatures were also featured in models M1 and M2. It might be of importance to notice how December and January

temperature variables featured in the models are such that illustrate the effect of single cold extremes whereas November variables can be interpreted to depict the duration of more mediocre cold temperatures. The lowest minimum temperatures during winters in Värriö are, after all, most likely to take place in December and January.

Analysis of the general trends in temperature variables (Tables 4 and 5) revealed how December and January were the months with the most profound warming by almost all featured aspects with the notable exception of the lowest daily minimum temperature in January. Winter moth might thus have increased potential for successful overwintering in the future. It is, however, hard to determine the significance of February temperatures as there was no significant warming observed in the analysis. Even more so as February can represent the post-diapausal egg stage with less defense against cold. Still, February temperatures were not treated as significant predictors by any of the three models.

Model M1 somewhat surprisingly emphasized the significance of the lowest daily minimum temperature observed in April. This variable was also featured in M2. It is interesting to speculate whether that variable might have something to do with mountain birch budburst phenology that would then mirror its effects on the successful development of winter moth larvae early on in the growing season (e.g. Fält-Nardmann et al. 2016). Single highest daily minimum temperature in March was also featured in M1. Jepsen et al. (2011) reported how warmer springs can increase the synchrony between mountain birch and scarce umber moth (*Agriopis aurantiaria* Hübner), another more southern geometrid expanding its range towards north. Better synchrony allowed it to thrive in environments traditionally out of its reach. As winter moth is also a southern emigrant, it too might be able to utilize earlier budburst to its benefit.

In conclusion, the modeling practice revealed a few different signals that could be interpreted to represent different effects of winter temperatures on population dynamics of winter moth. Minimum temperatures in December and January probably refer to the mortality caused by short term exposure to extremely low temperature, whereas temperatures of November and even March could be said to highlight the effect of cumulative exposure to temperatures below zero but not that close to the limits of extreme cold tolerance. Variables depicting temperatures in March and April might have something to do with the phenological synchronization between herbivore and its host plant.

### 4.4 Possible sources of error

The conclusions derived from time series can often be affected by what is outside of the temporal scope of the data. Time series capture only the events taking place within that certain period of time, and we must remain cautious if we want to treat the observed phenomena as rules we can apply to situations, areas, or points in time anywhere else. In the case of this study, cyclic population dynamics operating in roughly ten-year intervals are not the easiest of phenomena to represent with data spanning "only" 33 years. Had they collected even five more years of light trap data in Värriö, we could have captured one more population peak of autumnal moth, which in turn could have altered some of the conclusions presented here. The methods of time series analysis try to account for this kind of data limitations, but it is still good to keep them in mind when interpreting the results.

There are many slightly different schools of time series analysis with varying methods and practices in, for example, data preparation and transformation, detrending, and modeling. Utilizing different strategies can lead to somewhat different outcomes. Therefore, it is of high importance to document the analysis steps to allow for a critical review of each of them. The modeling approach used in this current study is not one of excessive sophistication, but rather a first step taken towards a complete outcome. The results should hence be interpreted with caution.

Overall, the cyclic population dynamic of geometrid moths is the outcome of numerous factors interacting with each other. It is complicated to isolate the effect of just one of them. Even when the regulatory effect of winter temperatures is clearly established in previous research, analyzing it separately from the other factors is something that needs to be considered when reviewing the obtained results. The best models would be such that considered a wide spectrum of different variables with established connections in the cyclic population dynamic phenomenon. However, such datasets or complete time series are few and far between.

### 4.5 Outcome of hypotheses

Based on the results of this current study, the following underlined hypotheses can be accepted.

**$H_0$**: Peak population densities of the two species do not occur simultaneously.

**$H_1$**: Peak population densities take place simultaneously.

The development of winter moth and autumnal moth population densities was discovered to be synchronous in a way that peak densities took place simultaneously without notable time-lags in the system. They were, however, not likely affected by each other per se, but rather reacted to other environmental factors in a similar manner.

**$H_0$**: There are species specific differences between the local distribution patterns based on elevation.

**$H_1$**: No distribution differences can be observed.

Results of this study support the hypothesized effect of elevation on species occurrence. Some effects are similar for both species while others are species specific. These results were established in analyses based on both altitude as a continuous variable and trap location as a nominal variable.

**$H_0$**: Winter temperature seems to be contributing to population dynamics of the species. There are also notable differences between the two species in this regard.

**$H_1$**: Winter temperature cannot be treated as a major factor determining the population dynamics of the species.

This study reported correlation between winter moth population density development and winter temperature variables. Such effect was not established for autumnal moth. Several recognized temperature variables operate through different mechanisms in the insect life cycle. However, winter temperature is only one of the numerous factors regulating the complex dynamic as a whole.

# 5. CONCLUSIONS

Mountain birch forest ecosystems of Northern Europe are likely to experience profound changes as a consequence of climate change. We need to understand the ecological and environmental mechanisms acting within these systems in order to be able to prepare for the consequences, try to hinder them in advance, or prevent them from happening all together. Even if the ecosystems are not of much commercial value (besides that of tourism), they have a key role in maintaining other vital ecosystem services and promoting unique biodiversity and livelihoods of many species. It is therefore important to reveal the consequences of climate change by e.g. analyzing and illustrating the development and trends in long-term ecological time series. The maintenance and funding of ongoing time series collection is currently of high importance.

As a result of this study, it can be concluded that environmental conditions in Northern Fennoscandia have changed since 1970s to such direction that promotes the success of winter moth populations in areas previously unsuitable for its more numerous occurrence. This study illustrated the development in a climatically more continental area, where even autumnal moth has not yet been able to produce regular outbreak cycles. Very similar results have been reported from the proper outbreak areas as well (see e.g. Jepsen et al. 2008). The declining trend of autumnal moth discovered in this study is not something that should be applicable to other locations without careful consideration on the mechanisms possibly responsible for this observed trend.

Ammunét et al. (2012) stated that lethal minimum temperatures for autumnal and winter moth eggs during diapause will be reached more and more seldom if climate change proceeds by its expected pace. Future studies should, however, acknowledge the different levels of cold hardiness of overwintering eggs at different phases of the cold season in order to produce more accurate modeling outcomes of the future developments. More field experiments on winter mortality are needed from the perspectives of not only single extreme temperatures but also prolonged exposure to temperatures capable of causing cumulative damage and, thus, increasing overall mortality. Such results cannot be obtained from sole lab experiments.

The current study acts as a steppingstone on the way to research the different ways winter temperatures regulate population dynamics and overall success of geometrid moths. This

goal can be reached by population development models that incorporate long ecological time series data with statistics on local weather conditions. However, it would be important to try take into account the precise microclimatic temperatures of an insect's winter habitat instead of using standard air temperature measurements conducted nearby (see e.g. Bale 1987). Temperature models with precise spatial resolution should be formed to be able to consider the temperature conditions at actual overwintering sites, since elevation and other habitat characteristics can create markedly different microclimates even in small areas (see e.g. Pepin et al. 2009). Using such models together with long-term climatic data would allow us to accurately find the most significant ways through which winter temperatures regulate the population fluctuations of geometrid moths.

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